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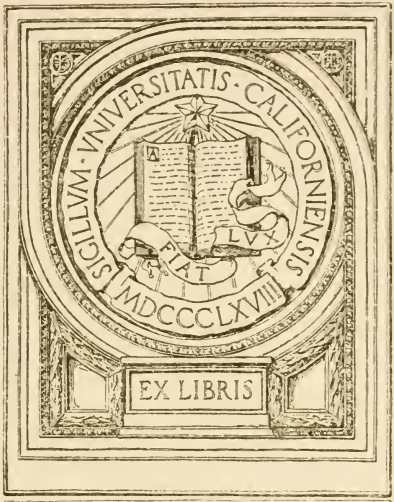

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A MANUAL OF VETERINARY PHYSIOLOGY.

ERRATUM.

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A MANUAL

OF

VETERINARY PHYSIOLOGY.

BY

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NEW YORK: W. R. JENKINS.

1892.

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TO

MICHAEL FOSTER, M.A., M.D., LL.D., F.R.S.,

PROFESSOR OF PHYSIOLOGY IN THE UNIVERSITY OF CAMBRIDGE,

THIS ATTEMPT TO DEAL WITH A BRANCH OF PHYSIOLOGY

IS DEDICATED,

IN ACKNOWLEDGMENT OF

ENCOURAGEMENT AND ASSISTANCE RENDERED TO

THE AUTHOR

IN PROSECUTING THE STUDY OF EQUINE PHYSIOLOGY.

259575

PREFACE.

My object throughout this manual has been to condense the information as much as possible, for which purpose I have omitted all special reference to the physiology of the dog, and have not touched upon the histology of the tissues, or methods of physiological inquiry.

The reasons for these omissions are obvious: special canine physiology is of subordinate interest to the profession, and our information about this animal is so complete, that no difficulty is experienced in obtaining it, when required, from human text-books. The histology of the tissues is already before the profession, and methods of physiological inquiry are only needed for laboratory work, for which purpose this book is not intended.

In the description of the physiology of the various organs and tissues, the horse is necessarily taken as the type; but the ox, sheep, and pig are dealt with wherever their special physiology requires it.

It was my original intention to publish nothing until I had gone over the field of equine physiology, but I found, after several years of work, that the information I had collected was a mere drop in the ocean, for inquiries of this

kind are necessarily slow, and as there appeared no reasonable prospect of covering within the space of one life the ground I had mapped out, I was advised that only good could result from placing on record what we do know of veterinary physiology.

I have, therefore, ventured, I know well how imperfectly, to state the broad facts of the science, so as to render them of use to the student and practitioner. The work does not pretend to be anything more than a stepping-stone to the study of physiology; for those requiring more detailed information, reference must be made to the various text-books of human and comparative physiology which are available.

Incomplete as the work is, it would have been still more so but for the assistance I have received from my friend Dr. Sheridan Lea, F.R.S., of Caius College, Cambridge, who, at great personal inconvenience, has kindly read and revised nearly all the sheets as they passed through the press. In saying this, and expressing to him my very great indebtedness, I in no way wish to shift the responsibility for error or inaccuracy which may exist, but I feel that whatever merit the book possesses is entirely due to him.

I have to thank Professor Michael Foster, F.R.S., for the loan of many of the woodcuts which illustrate this manual, and elsewhere I have acknowledged how much I owe to his encouragement.

To my friend and colleague, Assistant-Professor Butler, A.V.D., my best thanks are due for assistance in revising

the proofs, and in the preparation of the index; to Mr. W. Hunting, F.R.C.V.S., for suggestions on the chapter dealing with Locomotion; and to Professor M'Fadyean for the loan of two woodcuts illustrating the chapter on the Foot.

To facilitate the study of locomotion, I have had the plates so arranged as to face as nearly as possible the letterpress describing the movements.

I have laid under contribution Colin's invaluable 'Traité de Physiologie comparée des Animaux'; Ellenberger's 'Physiologie der Haussäugethiere'; Foster's, M'Kendrick's, and Landois and Stirling's Text-books of Physiology; Gamgee's translation of 'Hermann's Physiology'; the same author's 'Physiological Chemistry of the Animal Body'; Halliburton's 'Text-book of Chemical Physiology and Pathology'; Bunge's 'Physiological and Pathological Chemistry'; Meade Smith's 'Physiology of the Domestic Animals,' and others mentioned in the text. With reference to Dr. Meade Smith's work, I regret to find that on page 105 I have inadvertently given the title as 'A Text-book of Comparative Physiology.'

I have endeavoured to acknowledge all sources of information, though it is possible that, in drawing from such a wide area, I may have omitted in places to do so.

Army Veterinary School, Aldershot,
August, 1892.

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A MANUAL OF VETERINARY PHYSIOLOGY.

CHAPTER I.

THE CHEMICAL CONSTITUENTS OF THE ORGANISM.

Chemistry shows that a large number of the so-called elements enter into the composition of the body. Oxygen, hydrogen, carbon, nitrogen, sulphur, phosphorus, chlorine, fluorine, silicon, potassium, sodium, calcium, magnesium, and iron are found, not in a free state, or only to a very slight extent, but brought together in such a way as to form compounds, and these may be divided into two classes —Organic and Inorganic.

Before reviewing the compounds of the body, we may briefly notice the part played in nature by the various elements, and the methods by which these enter the bodies of animals; this is especially interesting to the veterinary physiologist, as, with few exceptions, the animals with which he has to deal, and of which this book mainly treats, obtain their store of the needful elements direct from the vegetable kingdom, instead of through the intermediate stage of the animal kingdom.*

Carbon exists in nature principally in the form of carbonic acid, viz., united to oxygen; it is only in this compound that it can be taken up by plants, which in their special laboratory split off the oxygen molecule and store up the

* Bunge, 'Physiological and Pathological Chemistry,' has been followed in this account of the elements of the body.

carbon, returning the oxygen to the air, and thus supplying to the atmosphere what animals are momentarily depriving it of. Even the solid carbon in the form of coal must at one time have been carbonic acid, for the reason just mentioned that this is the only form in which carbon can be taken up by plants. Carbon enters the animal system with the carbon of the food, and leaves it either as carbonic acid or in compounds, such as urea, which readily yield it; as carbonic acid, therefore, it is again taken up by the plant.

Hydrogen does not occur in the free state in nature, but principally as water, and a very small quantity as ammonia; in these forms the hydrogen is taken up into the plant, by which it is introduced into the animal, which gives it off again as water and ammonia, or a substance which readily yields these.

Oxygen is the most widely distributed of the elements, forming one quarter by weight of the atmosphere, and eight-ninths the weight of water; it also forms, by means of its compounds, one-half the weight of the earth's crust. It is the only element which enters the animal or vegetable body in a free state, and then only to a limited extent. We have mentioned the combination of carbon with oxygen, and it is this which principally supplies the plant with the oxygen required; at the same time the plant returning the oxygen to the air, maintains the needful balance which should exist between the carbonic acid and oxygen.

Nitrogen exists largely in a free state, no less than four-fifths of it being in this form in the atmosphere; it has but little affinity for other elements. In the form of ammonia, nitrous and nitric acids, it enters the plant, free nitrogen the plant cannot assimilate. In the form of vegetable proteid it enters the animal, leaving it as urea, etc., which by rapid decomposition yields ammonia. The animal cannot utilize free nitrogen any more than the plant, though the gas is found dissolved to a slight extent in some of the fluids of the body.

Sulphur exists largely in nature in combination as sulphates of alkalies and alkaline earths; in this form it

is taken up by the vegetable, and forming a part of the proteid molecule is taken into the body of the animal, where, by splitting up and oxidation, it yields sulphuric acid, in which form it is excreted by the urine.

Phosphorus enters plants as phosphoric acid united with alkalies; in soils it exists in only small quantities, hence the necessity of phosphates as manure. In the plant phosphoric acid forms a part of the complicated compounds known as lecithin and nuclein, in which condition it enters the animal body, forming a part of both the solid and fluid tissues.

Chlorine does not exist in a free state in nature but combined with potassium and sodium, in which form it enters plants and from these passes in the same compounds into animals.

Neither sodium, potassium, nor magnesium enter or leave the body or plant in any organic form, but simply as inorganic salts. Bunge considers that calcium may enter the body as an organic compound, his reasons for this view are mentioned later in this chapter.

Iron occurs free and in a ferrous and ferric state in nature; in the soil it permits the retention of carbon, and also enables it to return to the atmosphere. In the animal it is an oxygen-carrier, combined with a highly complex body known as hæmoglobin. It furnishes the vegetable with its colouring matter, for chlorophyll cannot be formed without it. It is not known in what form iron leaves the body.

Silicon, in the form of silicic acid, is taken up by plants, through the aid of which the stems, which largely consist of it, are capable of standing erect. Through the plant it is taken into the body and passes into the tissues. It is largely of use in the development of hair, and much of it passes out of the bodies of herbivora through the urine; in sheep, according to Bunge, it sometimes causes stone in the bladder.

Bunge, in his remarkably clear style, having thus traced the cycle of the elments from nature into the plant, from the plant into the animal, and from the animal back to nature again, then draws a contrast in the following terms between the changes occurring in the animal and vegetable:

1. The plant forms organic substances; the animal destroys organic substances. The vital process in the plant is synthetic, in the animal analytic.

2. The life of the plant is a process of reduction: the life of the animal a process of oxidation.

3. The plant uses up kinetic energy and produces potential energy: the animal uses up potential energy and produces kinetic energy.

Passing now to the organic and inorganic compounds found in the body, we find that the organic can be divided into nitrogenous and non-nitrogenous.

M'Kendrick* presents a table of the organic compounds prepared on a physiological classification, which is here reproduced.

I. Nitrogenous Bodies.

I.—Proteids.

A. True Albumins.

1. Albumins—Serum albumin (blood), and egg albumin.
2. Globulins—Vitellin (yolk of egg), myosin (muscle), paraglobulin (blood), and fibrinogen (blood).
3. Fibrin (blood-clot).
4. Proteins—Casein (milk), alkali albumin, syntonin or acid albumin (muscle).
5. Peptones—Albumin peptones, gelatin peptones (both digestive products).
6. Crystallizable albuminoids. Hæmoglobin (blood).
7. Soluble ferments—Ptyalin (saliva), pepsin (gastric juice), pancreatin (pancreatic juice), tripsin (pancreatic juice), inversive ferment (intestine), rennet (stomach of calf), lactic ferment (intestines), fat splitting ferment (pancreas), blood ferment.

B. Albuminates.

1. Collagen (yielding gelatin), chondrigen (yielding chondrin), elastin (from elastic tissue), keratin (from horn and epidermis), mucin (from mucus), and nuclein (nuclei of cells).

II. Fatty Nitrogenous Matters.

1. Phosphoglyceric acid, nervous matter.
2. Cholin or neurin, bile, etc.
3. Lecithin, nervous tissue, blood corpuscles, yolk of egg, etc.
4. Cerebrin, nervous tissues.

* 'Text-book of Physiology.'

Nitrogenous Bodies—*Continued.*

III.—Amides.

1. Urea, urine, etc.
2. Oxaluric acid, urine.
3. Allantoin, embryonic fluids.

IV.—Amido Acids.

1. Glycocolle, glycocin or glycin, bile, etc.
2. Leucin, pancreas, spleen, intestinal canal.
3. Tyrosin, pancreas, intestinal canal.
4. Creatin, muscles.
5. Creatinin, urine.
6. Taurin, muscles, lungs, fæces.
7. Cystin, urine.
8. Sarcosin, muscle.

V.—Nitrogenous Acids.

1. Sulphocyanic acid, saliva.
2. Uric acid, urine.
3. Hippuric acid, urine.
4. Inosinic acid, muscle.
5. Bile acids—glycocholic, taurocholic, and cholalic acids.

VI.—Salts formed by Organic Acids and Inorganic Bases.

1. Hippurate of soda, urine.
2. Hippurate of lime, urine.
3. Urate of soda, urine.
4. Urate of lime, urine.
5. Oxalate of lime, urine.
6. Glycocholate of soda, bile.
7. Taurocholate of soda, bile.
8. Sulphocyanide of potassium, saliva.
9. Phenolsulphate of potassium, urine.

VII.—Nitrogenous Bodies containing no Oxygen.

1. Trimethylamine, urine.
2. Indol, fæces.
3. Skatol, fæces.

VIII.—Pigments.

1. Blood pigments—hæmoglobin, hæmatin, hæmatoidin.
2. Bile pigments—bilirubin, biliverdin, choletelin, bilifuscin, biliprasin, hydrobilirubin.
3. Urine pigments—urobilin and indican.
4. Other pigments—lutein (yolk of egg), melanin (eye), sterco bilin (fæces).

II.—Non-nitrogenous Bodies.

I.—Alcohols.

1. Ethylic alcohol (muscle), cholesterine (bile and nervous tissues), glycerine (intestines), phenol (fæces and urine).

II.—Fats.

1. Tristearin, tripalmitin, triolein; soaps of these acids formed with potash and soda.

III.—Carbo-hydrates.

1. Glucoses—Dextrose, levulose, mannitose, galactose, inosite.
2. Sucroses—Sucrose (cane-sugar), lactose (milk-sugar), maltose.
3. Amyloses—Starch, glycogen, dextrin, inulin, gums, and cellulose.

IV.—Non-nitrogenous Acids.

1. Acetic Acid Series—Formic, acetic, propionic, butyric, caproic, palmitic, margaric, and stearic acids.
2. Glycollic Acid Series—Carbonic, glycollic, and lactic acids.
3. Oxalic Acid Series—Oxalic, succinic, and sebacic acids.
4. Aromatic Acid Series—Benzoic acid and phenol.

Proteids.*—This term has been applied to several substances more or less closely allied, which in one form or other go to make up by far the largest portion of the animal body. The proteids possess no definite chemical formula; they are highly complex substances, and have never, with some exceptions, been obtained in a crystalline condition; they are colloids—that is, they do not diffuse through an animal membrane—and they are substances which are not only indispensable to the body, but nothing else can even temporarily replace them.

The true type of proteid is the albumin found in blood, milk, eggs, etc., and these are true proteids, albuminous bodies, or albumins. Substances termed albuminoid, albuminate, albumose, albumid, proteose, etc, are not true albumins or proteids but only derivative bodies, in many respects closely allied to albumins, but possessing certain reactions which clearly distinguish them from true proteids.

* I am indebted to Halliburton's 'Physiological Chemistry,' M'Kendrick's and Landois and Stirling's 'Text-books of Physiology,' for this account of the chemistry of the body.

All proteids contain carbon, hydrogen, oxygen, nitrogen, and sulphur.

Carbon	-	50 to 55 per cent.
Hydrogen	-	6·6 to 7·3 ,,
Oxygen	-	19 to 24 ,,
Nitrogen	-	15 to 19 ,,
Sulphur	-	·3 to 2·4 ,,

In the animal body proteids undergo a breaking up, the complex body is resolved into simpler bodies, resulting in the production of such substances as leucin and tyrosin, and from these the proteids are eliminated as carbonic acid, urea, and water. The substances resulting from this breaking up are known as decomposition products.

Some albumins are soluble in water, others in saline solution strong or weak, and in this way it has been possible to classify the true proteids.

Albumins are soluble in water, in weak salt solution, and coagulated by heat; belonging to this class are serum, egg, muscle, and vegetable albumin.

Globulins (which are also true albumins or proteids) are insoluble in water, but soluble in dilute solution of common salt and precipitated by heat. In this class are found the globulin and fibrinogen of the blood plasma, also that found in the crystalline lens, the vitellin of eggs, etc.

Fibrin is a solid albuminous substance produced by a ferment in blood, chyle, and lymph; it is insoluble in water, but soluble in weak saline solution.

The **Derived Albumins** are obtained by the action of acids or alkalies on true albumins. These bodies are insoluble in water, but are soluble in dilute acid and alkalies, and in weak salt solution. They are not coagulated by boiling as the true proteids are. To this class belong acid albumin or syntonin, alkali albumin, and the albumin of milk, caseinogen.

If any of the above proteid bodies be acted upon by the gastric or pancreatic secretions, they undergo a change into a substance known as peptone; but before reaching the peptone stage they pass through an intermediate one known

as albumose, or, to follow Halliburton—whose authority on the nature of proteids is universally recognised—into a class he terms proteoses. This proteose class consists of albumoses, globuloses, vitelloses, caseoses, etc., depending upon the origin of the proteose, viz., whether from albumin, globulin, vitellin, casein, etc.; and after the proteids have passed through this stage they reach the final one of peptones. But the proteid group is still further complicated by the fact that there are different sub-varieties of proteose; albumose, for example, consists of three different kinds, known as proto, hetero, and deutero albumose, each giving a distinctive reaction: and the same remark applies to the others.

Peptones are not simple bodies, but consist of two forms hemi- and anti-peptone, the difference between them being that hemi-peptone under the action of the pancreatic fluid yields two substances leucin and tyrosin, whilst anti-peptone does not.

We have previously mentioned that the complicated proteid molecule is split up in the body into simpler compounds, and we have now seen how this occurs. The albumin taken in with the food is acted upon in the stomach by an acid and a ferment, converting it into proteose and then into peptone. The latter substance in the intestinal canal, under the influence of an alkali and a ferment, has a portion of it still further split up into leucine and tyrosin, and these two eventually assist to form urea, in which condition the bulk of the waste proteid of the body is excreted.

The vegetable proteids may be divided into the same groups as the animal proteids. The form in which the bulk of the proteid of plants occurs is as globulin, not albumin, which is the reverse of what obtains in the animal; the ultimate decomposition products of vegetable albumin in the system are the same as those of animal albumin.

The following table will probably help to render the classification of albumins clearer:

Albumins.
Serum albumin
Egg "
Muscle "
Acted upon by acids or alkalies yield
Acid albumin or alkali albumin
Under the influence of the digestive ferments and acids or alkalies these yield in the first instance
Proteose of the proto, hetero, or deutero variety
And next pass into peptone, which consists of
Hemi-peptone
Anti-peptone
Yields leucin and tyrosin
Yields neither leucin nor tyrosin.
Globulins.
Fibrinogen
Serum globulin
Globin
Myosinogen
Lense globulin
Albuminoids.
Gelatin.
Chondrin.
Mucin.
Elastin.
Keratin.
Yield urea.

Albuminoids are substances closely allied to albumins, but differing from them in some important particulars; they consist of such substances as gelatin, chondrin, mucin, elastin, keratin, and many others. These pass through the proteose and peptone stage in the same way as true albumins, but with certain differences.

The ordinary **Tests for Proteids** are based upon their precipitation by certain reagents, and in the same way it is possible to distinguish between one proteid and another. The most common test is the so-called xanthoproteic, obtained by the addition of a drop or two of nitric acid which produces a precipitate increased by boiling and turned yellow; albumoses are rendered clear by boiling with nitric acid and are thrown down again on cooling. If to the yellow fluid obtained by the action of nitric acid on an albuminous body a little ammonia be added, an orange colour is produced. Professor Halliburton regards this reaction as one of the most delicate we possess for proteids, we need hardly, therefore, go further than this for a test, although there are many other acids, organic and inorganic, salts of metals, neutral salts, etc., which act as precipitants, and to which reference will be found in text-books devoted to physiological chemistry; attention need here only be drawn to the fact that we are able to distinguish between serum albumin and globulin, and are also capable of separating peptones from other proteids, by the action of magnesium sulphate and ammonium sulphate.

A very remarkable fact about proteid substances is that though they constitute the mainspring of organic life, yet they number amongst them, or amongst their decomposition products, some of the most powerful poisons known. Snake poison is a proteid, and even the albumose formed during the peptic digestion of albumin is highly poisonous if injected into the circulation.

The **Ferments** come under the proteid classification: they are bodies possessing the most remarkable activity, and capable of inducing in other bodies with which they may be brought into contact, changes which result in the pro-

duction of entirely new substances. A common illustration of ferment activity is the yeast-plant, which is capable of producing out of sugar, alcohol and carbonic acid; its function is due to a living cell, and such a ferment is described as organized; micro-organisms, such as are found in the intestinal canal and other places, which are capable of producing great changes in the constitution of organic fluids, are also classed as organized, for example, the lactic acid ferment or bacillus, and the bacillus splitting up urea into carbonate of ammonia, etc. In the body another class of ferment exists, which, as it does not depend upon a living cell, is described as unorganized or soluble; such is the ferment which converts starch into sugar, the so-called amylolytic; the proteolytic or ferment converting proteids into peptones; the fat-splitting ferment, which breaks up fat into glycerin and fatty acids; the milk-curdling ferment of the fourth stomach of the calf; the fibrin-forming ferment of the blood, etc.: all these can by appropriate means be isolated from the various tissues which produce them.

Almost all dead tissues and organic fluids may act as starch-converting ferments.

Both the unorganized and organized ferments agree in so far as their general action is concerned. All of them are destroyed by raising the fluids containing them to a certain temperature; none of them appear to suffer, that is to be worn out or exhausted, by the amount of work they perform, and in consequence in each case a small quantity of them will produce as great an effect as a larger quantity.

The **Pigments** of the body are classed as proteids; comparatively little is known about them, though they are widely distributed and perform important functions. The best known animal pigment is hæmoglobin, the red colouring matter of the blood; it is of a proteid nature, yet crystallizable, and it also contains iron; it acts as an oxygen carrier, and is often spoken of as a respiratory pigment; it has several derivatives (see Blood), which supply the colouring matter of the bile, urine, and fæces. The next pigment widely distributed is the black pigment of the body, or

melanin; it occurs in the skin, hair, eye, and is the chief constituent of the melanotic tumours so common in the horse. There are several other pigments, but none so important as the above; from the lipochromes, or fatty pigments, is derived the visual purple of the retina.

Fatty Nitrogenous Matters.—Though true fatty matters contain no nitrogen, yet in the body there is found, especially in the nervous system and blood, a fat-like substance containing nitrogen known as lecithin, and other fatty nitrogenous matters known as phospho-glyceric acid, cholin or neurin, and cerebrin. Lecithin appears to furnish the majority of these substances, which are found not only in the animal but also in the vegetable body.

In the **Amide Group** we have the important substance urea, the chief end product of proteid decomposition in the system.

The **Amido Acids** are an important group, formed by the breaking up of proteids in the body, and are intermediate between these and their end products which are excreted with the urine. Glycocin is connected with one of the bile acids, and also with hippuric acid; leucin and tyrosin are formed by the pancreatic ferment from proteids; creatin and creatinin are probably connected with the formation of urea; and taurin is found in the bile in conjunction with cholic acid.

Of the **Nitrogenous Acids**, some are found in the urine, others in the bile. Sulpho-cyanic acid is said to occur in the saliva, though I have never detected it in the horse. Uric acid only occurs in herbivora when they are out of health; it is then one of the end products of proteid decomposition.

Hippuric Acid in the urine of herbivora takes the place of uric acid; it is not free but combined with potash or soda as hippurates of these bases. It is readily formed after partaking of benzoic acid. In animals it is said to be derived from cellulose; if this were its sole origin it is clear that it could not be looked upon as a proteid end product; it is possible, however, that proteid does furnish glycocole and

benzoic acid, the union of which in the body produces hippuric acid. For further remarks on this acid see the chapter on the Urine.

Bile Acids.—These probably originate from proteid decomposition in the body, being furnished by glycocin and taurin ; see Liver.

Another group of nitrogenous bodies also connected with proteid decomposition is characterized by the absence of oxygen. **Trimethylamine** has been found in the blood of the calf, and in urine. **Indol** and **Skatol** found in the fæces are due to the decomposition of proteids produced by pancreatic digestion. These bodies are closely connected with the indigo group, which, however, contains oxygen.

Indigo occurs in the urine of herbivora ; it is derived from indol, which by oxidation becomes indigo blue. In the urine indican is found united with potassium sulphate, and should skatol and indol pass by this channel they are united with the same salt.

The next great chemical group is the Non-nitrogenous.

Fat is composed of a mixture of glycerin and fatty acids . the latter are known as olein, stearin, and palmitin, the two latter form the solid fats ; olein and palmitin the more liquid fats. In the sheep and ox the fat is very firm, and stearin enters into its composition, whereas in the horse the fat is more fluid, and olein and palmitin are the chief components.

The amount of fat in the body must depend upon the feeding of the animal, and will obviously vary within extreme limits ; in individual tissues marrow has the largest amount—nerve, brain, milk, muscle, liver, bone, bile, and blood, have proportions which decrease in the order given.

Special fatty acids are found in butter and milk.

The change which the fats undergo in the alimentary canal is discussed in the chapter on Digestion, whilst the origin of fat in the body and its function is dealt with under Nutrition.

The **Carbo-hydrates** consist of several substances, which

appear to throw themselves into three distinct groups, viz., the glucoses, or grape-sugar class; the saccharoses, or cane-sugar class; and the amyloses, or starchy class.

Glucoses.	*Saccharoses.*	*Amyloses.*
+ Glucose.	+ Saccharose.	+ Starch.
– Levulose.	+ Lactose.	+ Glycogen.
+ Galactose.	+ Maltose.	+ Dextrin.
Inosite.		Cellulose.
		Gums.

The whole of these bodies contain carbon, hydrogen, and oxygen, the two latter being in the proportion to form water.

Glucose, also known as **Dextrose**, is found in fruit, and occurs in small quantities in blood, in certain tissues of the body, in the fluid surrounding the fœtus of herbivora, and the urine of the fœtal calf and sheep. Under the influence of yeast it yields alcohol and carbonic acid, and it may also undergo the lactic fermentation.

The **test for glucose** is Trommer's, also the fermentation test with yeast (see chapter on the Urine). There are several other tests for sugar which will be found described in any text-book on physiology.

The influence of sugar and other solutions in turning the ray of polarized light to the right or left is well known; in the classification given above the plus sign indicates that the ray is turned to the right, or dextro-rotatory; the minus sign to the left, or lævo-rotatory.

Levulose is obtained by heating cane sugar with mineral acids; it may also be produced in the body through the inversive ferment in the intestine; in either case the cane sugar becomes converted into equal parts of glucose and levulose, the one differing from the other by its behaviour to polarized light.

Inosite, or muscle sugar, is found in nearly all the organs of the body besides the muscles; it may also be obtained from plants, peas, beans, potatoes, etc.

The cane-sugar group may be converted into the glucose group in the manner just indicated, cane sugar forming

glucose and levulose, lactose or milk sugar forming galactose, and maltose forming glucose.

Maltose is an important substance, as it is the chief sugar formed in the body by the action of the diastatic ferment on starch. The inverting ferment of the intestine, as with lactose and saccharose, can convert it into glucose.

The **Amylose** or starchy group represents a large class of substances furnished by the vegetable kingdom, and the function of which as food is to afford the animal the fuel by which muscular energy is alone rendered possible. Starch does not exist in the animal body as a natural constituent; animal starch, or glycogen, is derived from vegetable starch, but glycogen is not a constituent of the body, only a something stored up in it.

Starch is insoluble in cold water, but under the influence of moisture the starch granules swell considerably; by boiling these burst and form a solution. If starch be heated it undergoes change, first into a substance termed dextrin, or British gum, and secondly into glucose; it may also be converted into glucose by heating with mineral acids; by the diastatic ferments of the saliva and pancreas starch is converted into maltose; in each case, viz., whether by mineral acids or ferments, dextrin is an intermediate product.

Starch gives the well-known blue reaction with iodine, but if it be acted upon so as to become converted into dextrin, a red colour, and not a blue, is obtained on the addition of iodine; if the process of conversion is carried still further to the stage of maltose or glucose, no colour is developed with iodine, but the presence of sugar is abundantly shown.

Dextrin was first discovered in the muscles of the horse; it is found in most plants, and its preparation from starch is alluded to above. In muscles it occurs as an intermediate stage in the conversion of glycogen into sugar.

Glycogen, or animal starch, is a carbo-hydrate found in the liver, muscles, blood-cells, etc., it is derived from starch, and stored up in the tissues for future use in a manner

fully explained in the chapter dealing with the Liver. It gives a port-wine red, and not a blue, reaction with iodine. In the form of starch it cannot be utilized by the system, it has, therefore, to become converted into sugar; in its transformation it behaves exactly as vegetable starch, first becoming changed into dextrin and then into glucose, not into maltose as starch is in the intestinal canal. The ferment of the salivary glands and pancreas can rapidly induce this change.

Cellulose is an important consideration for the veterinary physiologist, owing to the considerable proportion in which it exists in the food of the herbivora. Cellulose forms the cell-wall and woody fibre of plants; if subjected to the action of boiling dilute sulphuric acid it becomes converted into dextrin. It is generally believed that cellulose cannot be digested, but there can be no doubt that it is utilized by herbivora, though in what way it becomes converted we are not prepared to say. The cellulose ferment has yet to be discovered, but doubtless the large stomachs of the ox and the capacious intestines of the horse are intended for its dissolution and assimilation. Bunge states that experiments have proved that 60 per cent. to 70 per cent. of the cellulose disappears in the intestinal canal, and that sheep were capable of digesting 30 per cent. to 40 per cent. of the cellulose of sawdust and paper when mixed with hay. This authority also lays stress upon the important advantages derived from the use of cellulose, in mechanically stimulating the coats of the intestines and promoting natural peristalsis; all animals with a long intestinal canal need it, and if it be withheld from rabbits they die.

Gums.—A substance termed animal gum is found in mucus, and gives to it its peculiar ropiness. It yields a sugar which reduces salts of copper, but does not ferment.

The Alcohol Series in organic chemistry includes an interesting substance termed cholesterine, which is found in very many of the tissues of the body, more especially bile and brain. In the latter, small masses of cholesterine, exhibiting peculiar glistening fish-scale-like appear-

ance are regularly found about the cerebellum and in the ventricles; they form the substance of perhaps the majority of tumours seen in the brain of the horse. Cholesterine is also found in the wool of sheep united to a potash soap termed lanolin. The origin of cholesterine is unknown. Ethyl alcohol has been found in the muscles of the ox and horse.

Glycerin is found in fats, and, as previously mentioned, is liberated from them in the intestinal canal by the fat-splitting ferment of the pancreas; it has been supposed that the glycerin formed in the body contributes to the formation of glycogen.

Phenol, or carbolic acid, is largely formed in the intestinal canal of herbivora, due to the decomposition of proteid food the result of pancreatic digestion. It passes out of the body by the urine, united with sulphate of potash or combined in some way with sulphuric acid. This is the type of a number of bodies termed conjugate sulphuric acids, which are excreted by the urine, and to an extent form a measure of the amount of proteid decomposition occurring in the digestive canal.

Of the **Fatty** or **non-nitrogenous organic acids** there are several found in the animal body, such as formic, acetic, propionic, butyric, caproic, palmitic, and stearic. Acetic may be present in the digestive canal; propionic and butyric have been found in sweat, and as the latter acid is connected with lactic fermentation, it may be found wherever this is occurring. The palmitic and stearic acids have been noticed under the fats.

Several acids relating to the **Glycollic Series** are found in the body, the most important being lactic acid which is found in two or three different forms. It may occur in the stomach and muscles, and also results from fermentative changes in milk. The origin of muscle lactic acid is from glycogen or glucose.

The **Oxalic Acid Series** furnishes oxalic and succinic acids as occurring in the body. The oxalate of lime is common in herbivora, and results from the ingestion of vegetable food containing oxalates, also, perhaps, it is formed in the

body from proteids, sugar, etc. Succinic acid has been found in the urine after the ingestion of certain fruits containing malic acid and asparagin; it has also been found in some of the internal organs.

Inorganic Constituents.

The inorganic substances found in the body are water, gases, and salts. **Water** forms nearly 60 per cent. of the whole body; it is taken in with the food and drink, and a small quantity may be formed within the system.

The **Gases** of the body are oxygen, nitrogen, and hydrogen. The two former are taken in with the inspired air, while hydrogen is formed in the intestinal canal as the result of cellulose decomposition.

The largest portion of the inorganic matter consists of the various **Salts** of sodium, potassium, calcium, magnesium, and iron, in the form of chlorides, sulphates, phosphates, and carbonates. We find that the distribution of these salts throughout the tissues is very variable, some, like bone, are excessively rich, whilst others are remarkably poor in them. Certain tissues and fluids have a preponderance of some salts to the exclusion of others.

The amount of the salts existing in the body depends upon the age of the animal, and their nature is modified by the character of the food partaken of; the daily quantity ingested and stored up is largely affected by the rate of growth, young growing animals storing up mineral matter which the adult rejects.

In the composition of the milk we may obtain an insight into the nature and quantity of the salts required by growing animals. Bunge gives the following ash analysis of mare's and cow's milk:

	Cow's Milk.	*Mare's Milk.*
Potassium	1·76	1·04
Sodium	1·11	0·14
Calcium	1·59	1·23
Magnesium	·21	·12
Iron	·003	·015
Phosphoric acid	1·97	1·31
Chlorine	1·69	·31
Total ash per 1,000	7·97	4·17

The large amount of phosphoric acid and the preponderance of lime, afford us some explanation of the rapid growth of bone in the young of these animals; the large proportion of potassium and sodium in the cow, and the excess of potassium over sodium in the mare, are points more difficult of explanation, but bear out what I have yet to show, viz., the preponderance of potassium over sodium salts in the excretions of the horse.

Bunge compared the ash of a puppy with the milk of the mother, and the milk with the blood. It is remarkable how closely the composition of the puppy's system agreed with the salts it was receiving with the milk, though when the ash of the milk was compared with the ash of the blood of the mother, the greatest diversity in composition was apparent. This observer showed that the ash of the milk contained more potassium and less sodium than the ash found in the body of the young animal. We may also see that in cow's and mare's milk the potassium exceeds the sodium, and Bunge explains it by saying that as the animal grows it becomes richer in potassium and poorer in sodium salts, depending upon the relative increase in the muscular structure which is rich in potassium, and the relative decrease of the cartilaginous material which is rich in sodium.

In referring to Bunge's analysis of the cow's and mare's milk, one is struck by the small proportion of chlorine in the latter; I cannot offer any explanation why the calf requires so much more chlorine and sodium than the foal. The chlorides in the body are required not only for building up tissues, but in the production of secretions, and some considerable difference must exist in the constitution of the calf and foal to admit of such a difference in the amount of chlorine required.

Turning to the adult, we find that vegetable food furnishes considerably more potassium than sodium salts to the system, and Bunge's views about the muscle growth apply here also.

Sodium and Potassium.—Owing to the poorness of vege-

table food in sodium salts, Bunge believes that the administration of common salt with the food of herbivora is a necessity. As I hold different views on this important practical point, it is necessary that I should put forward his arguments in the matter, which I have here summarized.

In spite of the many inorganic salts found in the food, one only, viz., sodium chloride, is taken separately by the human subject, and in addition to that already existing in the food. But carnivora avoid salted food, as sufficient sodium chloride exists in the blood and tissues in the raw state in which these are consumed by them. Herbivora, on the other hand, have been known to travel considerable distances to obtain salt. Bunge explains this by saying that though the difference in the amount of common salt consumed by carnivora and herbivora is not very great, yet that herbivora consume three or four times as much potassium as carnivora, and he considers this latter fact accounts for the anxiety shown by them to obtain salt, for a reason to be presently explained.

In 1,000 parts of dried material, the following are the proportions of potassium and sodium found in certain articles of diet:

	Potassium.	*Sodium.*
Rice	1	·03
Bullock's blood	2	1·0
Oats, Wheat, Rye, Barley	5 to 6	·1 to ·4
Dog's milk	5 to 6	2 to 3
Peas	12	·2
Milk of herbivora	9 to 17	1·0 to 10·0
Hay	6 to 18	·3 to 1·5
Beef	19	3·0
Beans	21	·1
Clover	23	·1

For one equivalent of sodium the equivalents of potassium are:

	Equivalent K_2O.
Mangel-wurzel	2·0
Milk of herbivora	·8 to 6·0
Beef	4·0
Wheat	12·0 to 23·0
Barley	14 to 21
Oats	15 to 21
Rice	24
Rye	9 to 57
Hay	3 to 57
Peas	44 to 50
Clover	90
Beans	110

The preponderance of potassium over sodium salts is here most marked, and Bunge considers that when a relation of from 4 to 6 equivalents of potassium to one equivalent of sodium is obtained in a diet no addition of sodium chloride is necessary; but where the proportion of potassium is higher than this the animal instinctively seeks for sodium, for the reason that the effect of potassium salts in the blood is to withdraw sodium salts from the system.

I should be sorry to deny the stimulant to the palate which common salt may afford the herbivora, but so far as horses are concerned, and I think the same argument must apply to cattle, I am perfectly clear on the point that no addition of common salt to the ordinary diet is absolutely necessary, and that the food furnishes ample sodium, for the secretions, as shown by my inquiry into the amount excreted by the urine during rest and work, and the quantity excreted by the sweat.

From the little we know of the character of the saline secretions in the horse, we are prepared to find that the preponderance of potassium over sodium, in both the urine and the sweat, can only be accounted for by the excess of potassium salts supplied by the food.

Calcium forms the largest mineral deposit in the body; it is taken in by means of the food. Bunge states that it is probable that the lime salts required for the growth of bone in young animals are contained in some organic com-

pound, and that the administration of inorganic compounds of lime in rickets is irrational and useless.

Lime exists largely in clover and hay, but only in small quantities in the cereal grains; it is principally by the hay that the amount excreted by horses through the kidneys is supplied; it passes from the body in such quantities that it cannot be held in solution by the alkaline urine. In the body the calcium is in the form of phosphate, sulphate, and carbonate; in the urine as carbonate and oxalate.

Magnesium salts occur in the body principally as phosphates, and in this form they enter largely into certain foods, such as oats. The amount of magnesium passing away from horses through the kidneys is small, but considerable quantities derived from the food, and which cannot be utilized in the body, pass out with the fæces; by collecting in the bowels this salt produces the ammonio-magnesium phosphate calculi so common in horses.

Phosphates are united with soda, potash, lime, and magnesium. They are principally taken in with the food, but may also be formed in the body from the metabolism of phosphorus-containing compounds. The foods richest in phosphoric acid are oil-cake and bran, whilst hay and straw are poorest in this constituent. The combination of phosphates with magnesium has just been alluded to. Phosphoric acid is principally excreted by herbivora with the fæces, only small quantities passing away with the urine.

Carbonates are found in several of the secretions of the body, notably in the urine where they cause the most intense evolution of gas on the addition of an acid. The carbonates in the system of the herbivora result from the combustion of the organic acids, malic, citric, tartaric, etc., which enter the body as potassium salts, the potassium being set free and uniting with carbonic acid to form carbonate of potash; the potassium also unites with sulphuric acid, for which see sulphur.

The **Sulphur** in the body is derived from the albumin of

the food; in the system it is converted into sulphuric acid, and in this form 80 per cent. of the ingested sulphur appears in the urine. The sulphuric acid is united with the bases of the alkaline salts of vegetable acids, which, as just mentioned, are in the body converted by combustion into carbonates. These bases saturate the sulphuric acid, and it has been found experimentally that where the basic salts have been removed from the food, the sulphuric acid produced from the proteid attacks the bases forming part of the living body, and animals so fed die more rapidly than if starved (Bunge).

The importance of the sulphates in the urine is considerable; they afford a passage out of the body for the products of proteid change. Phenol and allied compounds are in this way got rid of in the form of phenol sulphate of potassium. Sulphur exists in horn, hair, and epidermis.

Iron is an important constituent of the complicated proteid hæmoglobin. It is also found in the hair, skin, bile, lymph, most body fluids and tissues, and a small quantity in the fæces. Bunge considers that the iron which enters the system can only be absorbed when in the form of an organic compound. Inorganic iron, though largely used in the treatment of certain diseases, is not absorbed from the intestinal canal; food contains only organic and not inorganic iron, and the hæmoglobin of the blood is formed from the complex organic compounds of iron which are produced by the vital process of the plant.

CHAPTER II.

THE BLOOD.

The special function of the blood is to nourish the tissues and to assist in removing from them the products of their activity. To enable this to be carried out, the blood is exposed in the lungs to the oxidizing action of the atmosphere, whereby the fluid which has recently been going the round of the body, and is highly charged with deleterious products, is once more revivified.

By means of a peculiar channel the circulation is placed in direct communication with the nourishing fluid absorbed into the body from the intestinal canal, by which process the blood is being constantly renewed.

Blood consists of a fluid portion known as the liquor sanguinis, floating in which are an immense number of solid particles known as corpuscles; it is the object of this chapter to point out how the liquor sanguinis and corpuscles are composed, and their various duties in the system.

Physical Characters of the Blood.—The colour of blood varies either as it is drawn from an artery or a vein; in the former it is of a bright scarlet colour, whilst in the latter it is of a bluish or purplish red. The colour of blood is due to a peculiar crystalline proteid known as hæmoglobin, and depending upon the condition of oxidation in which this is found is the scarlet or purplish colour obtained. Blood is opaque, owing to the manner in which the corpuscles found in it reflect the light, when these are destroyed the fluid becomes transparent; the liquor sanguinis is of a yellow colour.

The reaction of the blood is alkaline; this alkalinity diminishes in blood drawn from the body until the process of coagulation occurs. The alkaline reaction is due to the phosphate and bicarbonate of soda found in the fluid (Maly); the decreasing alkalinity observed on standing is probably due to the formation of an acid. The alkalinity of the blood is reduced by muscular work.

The odour of blood depends upon the animal it is obtained from. The blood of the cat and dog has a most disagreeable smell. This is not observed in the horse and ox, though, according to some observers, the odour of butyric acid can always be obtained by heating the blood with sulphuric acid. The taste of blood is saltish. The specific gravity varies in different animals; in the ox and pig, 1060; sheep, 1050-1058; dog, 1050 (Colin); horse, 1060; according to Hoppe-Seyler the specific gravity of the liquor sanguinis of the horse is 1027 to 1028, and the specific gravity of the cells 1105. The remarkable difference between the specific gravity of the cells and the liquor sanguinis in the horse accounts for the rapid manner in which the latter sink in blood drawn from the body, producing the so-called 'buffy coat.'

The **chemical composition of the blood** of animals will, as might be expected, possess almost absolute uniformity so far as the presence of various substances is concerned; the amount of these substances, however, both organic and inorganic, varies not only in animals of different classes, but in those of the same class; the composition of blood from an artery does not represent exactly that found in a vein. We will here content ourselves by enumerating the principal substances found in the blood, leaving the quantities of these to form a separate table at the end of the chapter.

Blood contains:

Liquor sanguinis or Plasma.
Red Corpuscles.
White Corpuscles.
Extractives.
Mineral matter.

It will be most convenient to deal with these in the order in which they are given.

The **Liquor Sanguinis**, or **Plasma**, forms about 66 per cent. of the total blood; it is a yellow albuminous fluid, containing at least three proteids, one of which may by certain processes be shown to be composed of two or three others. The proteids are:

Serum albumin, consisting of α, β, and γ albumins.
Serum globulin.
Fibrinogen.

During the life of the blood the liquor sanguinis is termed the plasma, but after it has been shed from the body, and coagulation has occurred, it is no longer described as plasma, but as serum; **Serum** is, therefore, plasma which is modified as the result of coagulation, and as this latter process is attended by the production of fibrin, we may say that serum is plasma minus the fibrin-forming elements.

The **Proteids of Serum** are serums albumin and globulin, and in addition there is the ferment produced as the result of coagulation; fibrinogen, having been used up in the process of coagulation, does not occur. The following table from Halliburton exhibits these points very clearly:

Proteids of the Plasma.	*Proteids of the Serum.*
Fibrinogen.	Serum globulin.
Serum globulin.	Serum albumin.
Serum albumin.	Fibrin ferment.

It has been shown that the proportion in which serum globulin and serum albumin exists in the blood varies in different animals; in the horse and ox the globulins are in excess of the albumins; in man and the rabbit this is reversed. The following table from Gamgee,* after Hammarsten, will render this clear:

* 'Physiological Chemistry.'

Variety of Serum.	Total Solids in 100 parts.	Total Proteids in 100 parts.	Serum Globulin in 100 parts.	Serum Albumin in 100 parts.	Lecithin, Fats, Salts, etc., in 100 parts.	Serum Globulin to Serum Albumin.
From blood of horse -	8·597	7·257	4·565	2·677	1·340	$\frac{1}{0·591}$
„ „ ox -	8·965	7·499	4·169	3·329	1·466	$\frac{1}{0·842}$
„ „ man -	9·207	7·619	3·103	4·561	1·587	$\frac{1}{1·511}$
„ „ rabbit -	7·525	6·225	1·788	4·436	1·299	$\frac{1}{2·5}$

The table shows that the amount of total proteids is more regular than the different albumins of which they are composed.

The specific gravity of the blood plasma is from 1027-1030, of the total weight of the blood it constitutes two-thirds, though, according to Bunge's analysis, the proportion of serum to total blood is not so large; he puts it down at 46·5 per cent. serum, and 53·5 per cent. corpuscles. Plasma possesses the power of clotting, yielding fibrin and serum. Sheep's blood yields more serum than any other (Halliburton).

Perhaps the nearest approach to pure plasma is the fluid found in the heart sac and abdominal cavity of the horse; even the pathological fluid of the chest, produced as the result of inflammation, is remarkably pure and free from white blood cells, and hence uncoagulable unless on the addition of a little fibrin ferment, when jellying shortly occurs.

Halliburton has shown by fractional coagulation that serum albumin may be composed of three other albumins, which he designates α, β, γ serum albumins. Strange to say that in the horse, ox, and sheep, no serum albumin α exists, but β and γ are present. Serum globulin (also known as paraglobulin and fibrino-plastic substance) exists in different proportions in the blood of domestic

animals; its greatest interest lies perhaps in the part it was supposed to play in the process of coagulation—a part which we have now good reason to believe does not exist. Fibrinogen is the precursor of fibrin in the blood—a substance we shall have more to say about in dealing with coagulation—it is found in blood plasma, but not in the serum; it also exists in the fluids thrown out into the cavity of the chest, pericardium, etc.

Corpuscles of the Blood.—Blood examined under the microscope is found to consist of an enormous number of bodies termed corpuscles floating in the liquor sanguinis. These corpuscles are found to be both red and white; the former are by far the more numerous, the latter are the larger.

The **Red Corpuscles**, viewed under the microscope, are biconcave discs, circular in shape, and possessing no nucleus, though, owing to their shape certain focussing may produce a dark centre which might be mistaken for a nucleus, but which is really due to the shape of the body, and is, therefore, an optical effect. The red cells have a tendency to lie on top of each other in the form of piles of pence, this condition is spoken of as forming rouleaux, and its cause is unknown. The circular shape of the red cell is affected by the amount of fluid in the blood: where the latter is small, as occurs in many diseases, the corpuscles become covered with spines or projections; when the fluid is in excess the corpuscles swell. The opacity of blood is due to the concave character of the corpuscles, reflecting light as from concave mirrors (M'Kendrick). When the corpuscles are destroyed the blood becomes transparent.

A red blood cell is composed of a stroma, holding in its meshes the red colouring matter. The stroma or framework of the corpuscle consists of an albuminous material allied to the globulins, and a fatty matter termed lecithin. The red colouring matter consists of an albuminous crystalline substance haemoglobin. The whole of these are contained in the corpuscle, not by means of an envelope, but retained in the pores of the stroma.

The number of corpuscles in the blood is approximately determined either by the method of Gowers, or Malassez. The principle on which these are based is the same—a known quantity of blood is diluted with a known bulk of artificial serum and accurately mixed; of this a small drop is placed in a counting-chamber, which is ruled into squares, and examined under the microscope. The blood cells occupying the squares are counted, which can readily be done, and the mean of them taken.

In the horse the mean number of red blood corpuscles per cubic millimetre* is 7,212,500, and in the ox 5,073,000. Taking the amount of blood in the horse at 66 lbs., this gives 204,113,750,000,000 as the approximate number of red cells in the body (Ellenberger).† They are increased by sweating, the excretion of water by the bowels and kidneys, and by starvation; they are diminished by pregnancy and copious draughts of water (Landois and Stirling).

Each red cell offers a certain absorbing surface for oxygen, which, if calculated on the total number of corpuscles, is something enormous, being equal for the horse to a square having a side of 140 yards.

By freezing and thawing the blood alternately, also by the addition of certain reagents to it such as chloroform, ether, bile salts, etc., the red blood cells can be so broken up as to liberate the colouring matter or hæmoglobin, which then deeply stains the serum, which is naturally yellow or colourless. The broken-up red cells do not now reflect light, and when this occurs the serum is seen of a red or laky colour and quite transparent; this is termed laky blood. Blood in its natural state, as previously mentioned, is opaque, but when treated by the above methods, or by electrical shocks, it becomes transparent.

The greater part of the red cell is hæmoglobin, a substance possessing a remarkable affinity for oxygen, which

* A cube having its edges about one-twenty-fifth of an inch.

† 'Physiologie der Haussäugethiere.'

it obtains at the lungs, and leaves behind it in the tissues. The hæmoglobin of the red cells, therefore, exists in two states, one in which it is charged with oxygen, called oxyhæmoglobin, and the other in which it has lost its oxygen, known as reduced hæmoglobin. The process of oxidation and partial reduction is constantly occurring at every revolution of the circulation, with the ultimate result that the red blood disc gets worn out and dies. In this condition it is cast off from the system, being got rid of through the medium of the liver as bilirubin, and also, probably, being destroyed in the spleen and elsewhere. When the red cells die their hæmoglobin is set free, and is decomposed into hæmatin, from which, probably, all the pigments of the body, but especially those of the bile, are formed.

The probable origin of the red cells is in the red marrow of bones; all other seats of formation appear doubtful. It is certain that their production is a matter of extreme rapidity, as may be witnessed, for example, after hæmorrhage. The red cells are not derived from the white. In the embryo the red cells are nucleated during the early period of development, but are gradually replaced by non-nucleated corpuscles before birth.

In speaking of the plasma, we mentioned the contradictory results obtained by various observers as to the proportion the plasma bore to the cells. According to some authorities, the blood cells are 35 to 40 per cent. of the weight of the blood. M'Kendrick gives the proportion of red cells as 33 per cent., or $\frac{1}{3}$; whilst Bunge, from an analysis of horse's blood, puts the red cells at 53 per cent., and the plasma at 47 per cent. It is probable that all these results were true for the specimen of blood examined, for there can be no doubt of the variation in the composition of this fluid.

We have mentioned that retained in the pores of the stroma of the red cells is the red colouring substance hæmoglobin, and with this we must now deal.

Hæmoglobin, also known as hæmato-globulin, and hæmato-crystalline, is a most remarkable body; it is a

proteid, yet crystallizes; whilst its behaviour in the dialyser is not that of a colloid but a crystalloid. It is one of the most complex substances in organic chemistry, and its molecule is a very large one. According to the analysis of Kosel,* hæmoglobin in the horse consists of:

C 54·87	O 19·73
H 6·97	S ·65
N 17·31	Fe ·47

The empirical formula for this body, on the assumption that the molecule contains one atom of iron, is given by Zinoffsky as follows:

$$C_{712}H_{1130}N_{214}FeS_2O_{245}.$$

Analyses have proved that oxy-hæmoglobin presents a perfectly constant composition, and is remarkable in being the only proximate constituent of the body containing iron.

The total amount of hæmoglobin in a horse's body is about 8·8 lbs.; and the amount of iron contained in this is about 257 grains. This calculation is based on the assumption that the amount of blood in the body is 66 lbs.

In the red blood cells hæmoglobin exists in the proportion of 86 per cent. to 94 per cent., whilst in the total blood of the horse it forms 13·15 per cent., in the ox 9·96 per cent., sheep 10·34 per cent., and pig 12·7 per cent. (Ellenberger).

The younger the animal the less hæmoglobin; males have more than females, and castrated animals more than entires (G. Müller).†

Hæmoglobin has a remarkable affinity for oxygen. The laws relating to the absorption of gases by fluids and solids do not apply to hæmoglobin. It has been calculated that 15½ grains of this substance will absorb 0·95 cubic inches of oxygen gas. We have mentioned that when hæmoglobin is charged with oxygen it is spoken of as oxy-hæmoglobin; when it has discharged its oxygen, which it is capable of

* Ellenberger's 'Physiologie der Haussäugethiere.' † *Ibid.*

doing with considerable facility, it is spoken of as reduced hæmoglobin. These, therefore, are its two conditions of oxidation: as oxy-hæmoglobin it is charged in the capillaries of the lungs, brought back to the heart and distributed all over the body; as partly reduced hæmoglobin it is produced in the tissues, and brought back by the veins to the heart for distribution to the lungs, where it renews its oxidized condition. Hæmoglobin is never completely reduced in the body, excepting in the last stage of asphyxia.

Oxy-hæmoglobin crystallizes in some animals, hare and guinea-pig, with facility; with others, ox, sheep, and pig, with difficulty. The crystals are generally rhombic plates and prisms; but the form differs according to the animal. Reduced hæmoglobin does not crystallize.

The two hæmoglobins produce quite distinctive spectra when examined by the spectroscope, by which they may be readily recognised. To put the matter roughly, oxy-hæmoglobin gives a well-marked double band in the green portion of the spectrum, one band being wide the other narrow; whilst reduced hæmoglobin gives one wide single band in the same position.

Oxygen and hæmoglobin are so lightly bound together that they are readily separated. The oxygen is given off if the blood be placed in a vacuum or boiled, or if it be brought in contact with indifferent gases—such as nitrogen and hydrogen. It is the facility with which hæmoglobin parts with its oxygen which enables the tissues to obtain it.

Hæmoglobin forms, according to some observers, three, according to others four, compounds with gases:

With oxygen it forms oxy-hæmoglobin and methæmoglobin.
„ carbonic oxide it forms CO hæmoglobin.
„ nitric oxide „ NO „

Oxy-hæmoglobin we have dealt with: the others, in a work of this kind, can only receive a short notice at our hands, though the subject is one which is full of interest.

Methæmoglobin is produced by allowing blood to be ex-

posed to the air until it becomes brown in colour and acid in reaction; this substance gives a three-banded spectrum, and parts from its oxygen with difficulty. In **Carbonic oxide hæmoglobin** the hæmoglobin is already saturated with CO, and so cannot carry oxygen to the tissues, thereby rapidly producing death. The blood of people who have died from CO poisoning is of a cherry-red colour, and yields the spectrum of CO hæmoglobin—viz., two bands very much like those of oxy-hæmoglobin, but situated nearer to the violet end of the spectrum. **Nitric oxide hæmoglobin** in many respects resembles CO hæmoglobin.

Hæmoglobin may be decomposed either by boiling or the addition of alkalies, acids, or acid salts; in either case it splits up into a substance containing all the iron of the hæmoglobin, and known as **hæmatin**, and a proteid substance or substances termed **globin**.

Hæmatin has a metallic lustre, blue-black colour, is free from crystalline formation, and yields a dark-brown powder when pulverized; it contains 8·82 per cent. of iron. Hæmatin presents a distinctive spectrum, both in an acid and alkaline solution.

When hæmatin is boiled with glacial-acetic acid it yields **hæmin**, which, microscopically, is found to consist of prismatic crystals, dark, or nearly black in colour. Hoppe-Seyler considers this substance to be hydrochloride of hæmatin. The ready production of hæmin crystals by warming the blood with a drop of acetic acid on a slide is used as a microscopical test.

There are other derivatives of hæmatin, such as **Hæmochromogen**, which is a reduction product; **Hæmatoporphyrin**, which is hæmatin from which the iron has been removed; **Hæmatoidin**, found in old blood-clots and in the ovary, it is an iron free product of hæmatin, and gives the same reaction with nitric acid as bile pigment, viz., a play of colours. Hæmatoidin is, in fact, identical chemically with bilirubin.

The **White Corpuscles**, also termed leucocytes, are found in blood, lymph, pus, connective tissue, etc. They exist in

blood in the proportion of 1 to 335 of red (Landois and Stirling), but vary in their proportion according to the vessel from which the blood is examined. In the splenic artery there are very few, in the splenic vein they are exceedingly numerous. Blood which has been removed from the vessels contains but few, for the reason that they are probably broken down during the formation of fibrin. The white corpuscle is much larger than the red, and consists of what is known as protoplasm, which is granular in appearance; it possesses a nucleus or nuclei, and is endowed with movement; there is no cell-wall or envelope, but the body is made up of delicate fibrils, and the nucleus the same.

The movements, known as amœboid, exhibited by these corpuscles are remarkable, they are shown by changes of form, projections shooting out from the surface and being again retracted. The corpuscle has also the power of taking up small particles of colouring matter, bacteria, etc., into its interior. The amœboid movement is destroyed by heat, and by shocks from an induction coil.

The white corpuscles contain about 10 per cent. of solids, which consist of serum globulin, serum albumin, and myosin, or its precursor, myosinogen, as myosin probably only occurs after death. Another nitrogenous principle is nuclein, which is largely found in the corpuscle; it is remarkable for containing phosphorus. Besides these we have the complex fatty body lecithin, cholesterin, glycogen (especially in the horse), and salts, the latter principally phosphates probably derived from the phosphorus containing compounds.

The origin of the white corpuscles is from the lymphatic system, by which they enter the blood stream through the large lymphatic channels opening into the vena cava at the junction of the two jugular veins. The white corpuscles, as well as the red, are constantly being used up and as constantly replaced. This using up consists in the power they possess of passing through the walls of the vessels into the surrounding tissues, from which they are removed by the lymph channels, and so find their way back to the blood.

Pus consists largely of white cells collected in the tissues and forming an abscess.

No doubt many corpuscles leave the blood the destruction of which we are unable to account for, but it is probable, as suggested by Michael Foster, that by their death they influence the composition of the blood plasma, as in this fluid their component parts must become dissolved after their death.

During the life of the white corpuscle great activity prevails, it is constantly giving up and taking in material which must affect the composition of the plasma. We know that the white cell possesses the power of digesting certain substances, both solid and liquid. The researches of Metschnikoff have paved the way towards a better understanding of the probable way in which protection against certain diseases is obtained. The white cells digest the bacteria, taking them up into their own substance; it is a fight between bacteria and leucocytes; the protection afforded to the system by the white blood-cells is therefore not the least important of the functions performed by them.

On the death of the blood the white cells yield the so-called fibrin ferment, which produces the clotting of the blood.

A **Third Corpuscle** is described as found in the blood, termed by Hayem **Hæmatoblast**, and by Bizzozero **Blood-plate.** Their function and nature is unknown, though according to some they take an active part in that obscure process the clotting of the blood. Blood-plates are found in large numbers in the white thrombi found in vessels, and they may be readily obtained by passing a thread through a blood-vessel, or suspending threads in freshly-drawn blood (Bizzozero, Stirling). Semmer calls these plates red granular corpuscles; he states that they exhibit amœboid movement, and has examined them in the blood of the horse and other animals (Gamgee).

Coagulation.—We are now brought to a consideration of the subject of blood clotting, a process by which the naturally fluid blood becomes converted into a solid.

If blood be drawn from the body and left at rest, it will be found within a few minutes to have undergone the process of clotting, the fluid first becomes a jelly, and then a firm clot or crassamentum, taking a complete cast of the vessel in which it is placed, and so firm in consistence that the vessel may be inverted without any blood being lost. In a short time on the surface of the clot fluid may be seen which has been produced by the process of contraction, and in the course of a few hours the clot commences to sink in the now abundant blood-coloured serum which has collected as the result of this process. The blood of the horse is remarkable for the slow rate at which coagulation occurs, and the red cells being specifically heavier than the plasma have time to fall in the fluid before the process is completed, the result being that the upper solid layer is considerably decolourized, forming the so-called **Buffy coat**, which though natural to the horse, is indicative in other animals of the presence of an inflammatory process in the system.

I have here closely followed the account given by human physiologists of the coagulation of the blood in the horse, but the appearance described is by no means invariable; coagulation of the blood in this animal is often complete in less than five minutes, when, of course, no buffy coat forms, and I am inclined to believe that when life is instantaneously destroyed, and blood at once drawn, that rapid coagulation and non-buffy coat is the rule rather than the exception. The fluid drawn during life in many cases also clots with extreme rapidity.

The time occupied in coagulation varies in man from two to six minutes; in the horse Colin puts it at from fifteen to twenty-five or even thirty minutes, the same observer putting the sheep and dog at four to five minutes, and the ox at eight minutes. In my experience the time mentioned for the horse is exceptionally long.

If we examine the clot microscopically, it is found to consist of fine fibrils entangled in which are the blood corpuscles; if the fibrin produced be washed completely

free from blood, its appearance is well described by its name.

If instead of allowing the blood to clot spontaneously it be whipped with a rod or bunch of twigs, the fibrin separates rapidly and coats the rod, whilst coagulation in the remaining fluid is absolutely prevented. The power of spontaneous clotting lies then in the production of fibrin.

These changes may be graphically represented thus:

Clotting.

Blood. { Plasma. { Serum. / Fibrin. } / Corpuscles. { Red. / White. / Blood platelets. } } Clot.

(HALLIBURTON.)

When Whipped.

Blood. { Plasma. { Fibrin. / Serum. } / Corpuscles. { Red. / White. / Blood tablets. } } Defibrinated blood.

Fibrin is a yellowish-white, stringy-looking bulky mass; it may be dissolved by hydrochloric acid forming acid albumin or syntonin; also by dilute alkalies with the production of alkali albumin. Its general appearance would lead to the belief that it exists in blood in large quantities, it is found, however, to be by weight relati small; in human blood its proportion is ·2 per cei sheep, ·2 to ·3 per cent.; ox, ·3 to ·4 per cent.; hor ·4 per cent.; pig, ·4 to ·5 per cent. (Colin).

Fibrin is produced by the action of the **fibrin ferment** on fibrinogen, the whole of the latter being used up in the process. The ferment does not exist in living blood, but is produced by the disintegration of the white corpuscles immediately the blood is shed. Schmidt's view that fibrin can only be produced by the action of the fibrin

ferment on fibrinogen and serum globulin is held to be against the weight of evidence, which points to the presence of serum globulin as being unnecessary to coagulation.

The presence of neutral salts is necessary for the conversion by means of the ferment of fibrinogen into fibrin; no fibrin can be produced in their absence. Calcium sulphate appears to be the essential salt.

The **Theories of Coagulation** are very diverse, whilst Schmidt, as mentioned above, considered that the presence of fibrinogen, serum globulin, and the fibrin ferment, were all necessary to the process of clotting, Hammarsten considered that the globulin was unnecessary. Wooldridge believed that a substance found in the white corpuscles, lecithin, diffused into the plasma and produced clotting. In all cases, however, it was recognised that the salts of the blood were absolutely essential to the process.

The term 'ferment' in connection with fibrin ferment, is used more as a convenient expression than as an actual statement of its action; it is considered doubtful whether it 'splits up' fibrinogen into fibrin, and this it would probably do if a ferment.

It appears to be quite clear that fibrinogen and the fibrin ferment are the important factors in coagulation, for if a solution of fibrinogen be prepared in a pure condition, it will clot on the addition of the ferment, even though serum globulin be absent, the fibrinogen by itself being non-coagulable; conversely, if fibrinogen be removed from a fluid the latter will not coagulate even on the addition of the ferment. Certain pathological fluids, serum from the chest, etc., may be made to coagulate on the addition of a little washed blood clot, which contains the ferment in considerable quantities. Experiments made by injecting into the vessels of animals the active fibrin ferment, do not lead to coagulation of the blood in the vessels as we might suppose; the ferment is either destroyed, or else fibrinogen is not present; the former is the most likely.

It is a matter of common observation, that after death the coagulation of blood in the vessels is a slow process, though by exposure to the air clotting is almost at once produced; it was supposed that the air in some way influenced this, but it has been shown that the action is rather due to the influence on the blood exerted by the wall of the vessel. The jugular vein of a horse has been included between ligatures and excised, nevertheless the blood has remained fluid in it for one or two days, though suspended in such a way as to be left freely exposed to the air, yet on removal from the vein clotting will at once occur; while suspended the corpuscles sink, and it is found that the serum in the upper layer has considerably lost its power of coagulation, though the blood drawn from the lower stratum clots readily; evidently the corpuscles take an active part in the production of clotting. This was the view held by Schmidt, who maintained that the white corpuscles were rapidly dissolved in the plasma, in the horse to the extent of 71·7 per cent., and that the result of this dissolution was serum globulin and the fibrin ferment.

When blood-vessels are injured during life, or when pathological changes occur in the blood, coagulation in the vessels will occur.

Clotting in dead blood may be retarded or hastened by certain conditions. Blood of a horse received into a vessel so constructed as to expose it to a freezing temperature may be kept fluid for an indefinite period, though coagulation will at once occur when the temperature is allowed to rise.

The addition to the blood in certain proportions of the neutral salts of the alkalies and earths, ammonia, and sulphate of magnesia delay clotting; the addition of acetic acid and a current of CO_2 by precipitating the fibrinogen entirely prevent it, (venous blood which is rich in CO_2 is slow in clotting). By rapidly heating blood to 133° F. clotting is prevented, owing to the precipitation of the fibrin-forming substances; the addition of oil also retards clotting. The shape of the vessel in which the coagulating

blood is contained has an effect on the rapidity of the process: a deep vessel retards coagulation, whilst a rough and shallow one promotes it.

The **Extractives of the Blood** are fats, cholesterin, lecithin, creatin, urea, hippuric and uric acids, grape sugar in small and varying quantities. Fats occur as neutral fats, olein, stearin, and palmatin. The amount of fat in the blood during digestion is ·4 to ·6 per cent.; in fasting animals, ·2 per cent.; in dogs fed on a fatty diet it may reach 1·25 per cent. (Landois and Stirling). Schmidt states that there is twice as much fat in the serum of recently fed horses as in the serum of those kept starving. Soaps to the extent of ·05 per cent. to ·1 per cent. are found; urea, ·02 to ·04 per cent.; sugar, ·1 to ·15 per cent. Bilirubin has been found in the serum of the blood of calves (M'Kendrick).

The **Difference between Arterial and Venous Blood** is that the former contains more oxygen and less CO_2; arterial blood also contains more water, fibrin, extractives, salts, and sugar, fewer blood corpuscles, and less urea; its temperature is, on an average, 1° C. lower (Hermann).

The dark colour of venous blood is not due to the greater amount of CO_2 it contains, but to the diminution of oxygen in the red blood-cells. The alteration in colour effected by the addition of reagents and gases to blood, is probably due partly to alterations in the shape of the corpuscles themselves, which become more concave on the addition of oxygen and less concave on its removal; and to the fact that oxy-hæmoglobin is brighter than reduced.

The **Salts** of the blood are divided between the plasma and the corpuscles; the distribution of the salts in these is not the same in all animals; in the horse and pig, for example, sodium only exists in the plasma and none in the corpuscles, whereas in the ox and dog both corpuscles and plasma contain sodium; the salts of the red cells in man and the pig consist principally of potash, chlorides, and phosphates; in the ox potash and phosphates are small, lime is absent, whilst soda is large. In this connection the following table from Gamgee is interesting:

TABLE SHOWING THE AMOUNT OF POTASSIUM, SODIUM, AND CHLORINE PRESENT IN 100 PARTS OF THE INORGANIC MATTERS OF BLOOD CELLS AND PLASMA.

	Blood Cells.			*Liquor Sanguinis.*		
	K.	Na.	Cl.	K.	Na.	Cl.
Man -	40·89	9·71	21·00	5·19	37·74	40·68
Dog -	6·07	36·17	24·88	3·25	39·68	37·31
Cat -	7·85	35·02	27·59	5·17	37·64	41·70
Sheep -	14·57	38·07	27·21	6·56	38·56	40·89
Goat -	37·41	14·98	31·73	3·55	37·89	40·41

To this we may add, from Bunge's observations, for the horse, ox, and pig :

	1,000 *grammes of Corpuscles contain*			1,000 *grammes of Serum contain*		
	K.	Na.	Cl.	K.	Na.	Cl.
Horse -	4·92	0	1·93	·27	4·43	3·75
Ox - -	·747	2·093	1·635	·254	4·351	3·717
Pig - -	5·543	0	1·504	·273	4·272	3·611

According to C. Schmidt the blood contains chlorides, sulphates, phosphates, potassium, sodium, calcium phosphate, magnesium phosphate, and iron, which latter is contained in the hæmoglobin. There is no iron in the serum of the blood of any animal. The blood analyses quoted at the end of this chapter will give some idea of how these salts are distributed, and the proportion in which they exist.

The use of the salts is to assist in secretion, repair, and disintegration. The growth of the solid tissues of the body absolutely depends on the inorganic material supplied by the blood.

Water free from salts is destructive to protoplasm, no doubt, therefore, one important function of the salts in the blood is to maintain the vitality of the tissues. Sodium chloride is here especially valuable, and its extensive

presence in blood (60 per cent. to 90 per cent. of the total amount of ash) corresponds to its importance. As the blood is simply the carrier of the salts, and the only means by which the tissues can obtain them, it by no means follows that all the mineral matter found in it is essential to its own repair and constitution.

The **Quantity of Blood in the Body** can only be estimated approximately; direct bleeding alone does not furnish us with a true result; after all the blood is drained off, the vessels require to be washed out, and the quantity of blood in the water estimated by the colour present; the body has then to be minced and macerated, and the quantity of blood in this estimated by the colour test, comparison being made with a standard solution of blood.

According to Colin the weight of blood in the body of oxen is 39 lbs.; horses, 47 lbs. (35·2 pints); sheep, 4½ lbs.; pigs, 3 lbs. Sussdorf,* quoting recent experiments, puts the proportion which the weight of the blood bears to the body weight as being, for the horse, $\frac{1}{15}$; sheep, $\frac{1}{12}$; pig, $\frac{1}{22}$; ox, $\frac{1}{13}$.

The same observer quotes the amount of blood in the body of the horse at 66 lbs., or nearly 50 pints.

The **Distribution of Blood in the Body**, according to Ranke, is as follows:

About one-fourth in the heart, lungs, large vessels, and veins.
,, ,, liver.
,, ,, skeletal muscles.
,, ,, other organs.

It is probable that in the horse the liver would contain less than one-fourth the bulk of blood, whilst the skeletal muscles would contain more.

The abdominal veins are capable of containing the whole of the blood in the body. When an organ is active, it receives from 30 per cent. to 50 per cent. more blood than when at rest (M'Kendrick).

The Gases of Blood.—The blood gases are obtained by introducing the fluid into a Toricellian vacuum, the instrument used to obtain it being a mercury pump. In a

* Ellenberger's 'Physiologie der Haussäugethiere.'

vacuum the blood froths up and gives off its gases, which are then collected and analysed.

The gases found are oxygen, carbon dioxide, and nitrogen. The proportion of these found depends upon whether the blood be taken from an artery or a vein; in the former the oxygen is much larger than in the latter, and the carbonic acid less. The nitrogen in both cases practically remaining the same.

At a pressure of 30 inches of the barometer and a temperature of 32° F., the following gases are found in 100 volumes of blood:

	Arterial.	*Venous.*
Oxygen - -	20	12
Carbonic acid -	40	45
Nitrogen - -	2	2

The exact amount of gas varies. The above are mean quantities.

Oxygen exists in arterial blood in the proportion of about 20 per cent.; whilst in venous blood the proportion is found to vary within wide limits, depending upon the vessel from which it is taken.

Carotid artery, O 21 per cent. Renal vein (kidney active), O 17 per cent.
Renal „ „ 19 „ Renal „ (kidney passive), „ 6 „
(Landois and Stirling.)

In the blood of asphyxia oxygen is nearly absent.

It will be remembered that by far the greater part of the oxygen is in combination with the hæmoglobin of the red blood corpuscles. It has been determined that 15½ grains of hæmoglobin is capable of absorbing ·95 cubic inches of oxygen. The serum of blood contains the oxygen simply absorbed, the amount held in solution is therefore small. The oxygen chemically united with the hæmoglobin is quite independent of the laws which regulate the absorption of gases (see Respiration).

Besides the vacuum of the air-pump, various chemical substances have the power of deoxidizing the blood-cells, such reducing substances are ammonium sulphide, sul-

phuretted hydrogen, iron salts, etc. The proportion of oxygen in the blood bears a relation to the amount of iron contained by the hæmoglobin.

Blood exposed to the air loses oxygen, due to decomposition leading to the production of reducing substances.

It has been supposed, owing to the readiness with which hæmoglobin parts with its oxygen, that the latter must be in the form of ozone (Hermann); but this view is, however, incorrect.

The **Carbonic Acid** in arterial blood is about 39 per cent.; in venous blood it varies, depending on the vessel. The CO_2 is principally united to the sodium carbonate in the plasma of the blood.

The **Nitrogen** in the blood is small in amount, about 2 vols. per cent.; it does not vary in arterial or venous blood, as in both cases it is simply absorbed by the plasma; though Fernet and Setschenow* consider that a small portion of it is chemically combined in the blood-cells.

Chemical Composition of the Blood.—The following are the analytical tables of the blood of animals furnished by various authors. I have omitted a very large series given in Simon's 'Chemistry,' from analyses made by Nasse, and also Lehmann's analyses, published in his 'Physiological Chemistry,' as the results do not compare with those obtained in more recent periods, by probably more accurate methods of inquiry:

HORSE.

100 *parts by weight of blood contain:*

Blood corpuscles,	34·418,	containing	12·8 per cent. of solids.
Plasma,	65·582,	„	10·0 „ „

(C. SCHMIDT, LANDOIS, AND STIRLING.)

100 *parts of venous blood contain:*

Corpuscles - - -	32·6 per cent.
Plasma - - - -	67·4 „

The corpuscles contain:

Water - - - -	56·5 per cent.
Solid matter - - -	43·5 „

* Hermann's 'Human Physiology' (Gamgee).

HORSE (*continued*).

The plasma contains:	
Water	90·8 per cent.
Solids	9·2 „
The solids consist of:	
Fibrin	·4 per cent.
Albumin	7·5 „
Fat	·1 „
Extractives	·4 „
Soluble salts	·6 „
Insoluble salts	·2 „

(HOPPE-SEYLER AND HERMANN.)

PERCENTAGE COMPOSITION OF BLOOD.

	Horse. (Hoppe-Seyler.)	*Ox.* (Bunge.)	*Dog.* (Hoppe-Seyler.)
Blood corpuscles	33·45	31·87	35·70
Solids	13·03	12·75	15·38
Water	20·42	19·12	20·32
Plasma	66·55	68·13	64·30
Solids	6·50	5·91	5·60
Water	60·05	62·22	58·70

(M'KENDRICK.)

1,000 PARTS BY WEIGHT OF DEFIBRINATED BLOOD CONTAIN

	PIG.		HORSE.		OX.	
	436·8 *Corpuscles.*	563·2 *Serum.*	531·5 *Corpuscles.*	468·5 *Serum.*	317·7 *Corpuscles.*	681·3 *Serum.*
Water	276·1	517·9	323·6	420·1	191·2	622·2
Fixed substances	160·7	45·3	207·9	48·4	127·5	59·1
Albumin and hæmoglobin	151·6	38·1	—	—	123·6	49·9
Other organic substances	5·2	2·8	—	—	2·4	3·8
Inorganic substances	3·9	4·3	—	—	1·5	5·4
K_2O	2·421	·154	2·62	·13	·238	·173
Na_2O	0	2·406	0	2·08	·667	2·964
CaO	0	·072	—	—	—	·070
MgO	·069	·021	—	—	·005	·031
Fe_2O_3	—	·006	—	—	—	·007
Cl	·657	2·034	1·02	1·76	·521	2·532
P_2O_5	·903	·106	—	—	·224	·181

(BUNGE.)

	1,000 Parts by Weight of Corpuscles Contain			1,000 Parts by Weight of Serum Contain		
	Pig.	Horse.	Ox.	Pig.	Horse.	Ox.
Water	632·1	608·9	599·9	919·6	896·6	913·3
Fixed substances	367·9	391·1	400·1	80·4	103·4	86·7
Albumin and hæmoglobin	347·1	—	387·8	67·7	—	73·2
Other organic substances	12·0	—	7·5	5·0	—	5·6
Inorganic substances	8·9	—	4·8	7·7	—	7·9
K_2O	5·543	4·92	·747	·273	·27	·254
Na_2O	0	0	2·093	4·272	4·43	4·351
CaO	0	—	0	·136	—	·126
MgO	·158	—	·017	·038	—	·045
Fe_2O_3	—	—	—	—	—	·011
Cl	1·504	1·93	1·635	3·611	3·75	3·717
P_2O_5	2·067	—	·703	·188	—	·266

(Bunge.)

These tables do not compare very well, but as the analyses were made by men whose results are of undoubted accuracy, they are interesting as showing how the blood may vary in composition.

Reviewing these analyses, we may say that dividing the blood into corpuscles and plasma, that the latter consists of—

Water	90 parts per cent.
Proteids	8 or 9 parts.
Fats	·1 „
Fibrin	·2 or 4 „
Extractives	·4 „
Salts	·8 „

The Corpuscles.

Water	56 parts.
Solids	43 „ consisting of 90 per cent. hæmoglobin, 8 per cent. proteids.
Salts	1 „

CHAPTER III.

THE HEART.

The blood in the body has to be kept in constant motion in order that the tissues which are depending upon it for their vitality may be continuously supplied, and also in order that the impure fluid resulting from these changes, may be rapidly and effectually conveyed to those organs where its purification is carried out.

The heart is the organ which pumps the blood over the body, not only distributing it to the tissues, but forcing it on from these back to the heart again to be prepared for redistribution. It may be described as a hollow muscle divided into two compartments, right and left, each compartment being capable of division into an upper one or auricle, and a lower or ventricle. Opening into the auricles are large veins which convey the blood back from the body for redistribution by the ventricles; the two cavities are separated by a valvular arrangement. From the ventricles other vessels, arteries, take their origin for the conveyance of blood from the heart.

So far the general arrangement of both right and left sides of the heart are much the same, each having to receive and then to get rid of a certain quantity of blood pumped into it; but the blood pumped into the right heart is very different from that pumped into the left, and it is with these differences that we must for a moment deal.

Into the right heart the whole of the impure or venous blood in the body is brought, for the purpose of being purified in the lungs; into the left heart the

arterial or purified blood is brought back from the lungs for distribution over the body. The former is often called the Pulmonic, the latter the Systemic circulation.

Mention has been made of valves in the cavities of the heart; we find them on both right and left sides separating auricle from ventricle, known as the right auriculo-ventricular or tricuspid valve, and the left auriculo-ventricular or mitral valve. Besides these, valves are found in the vessels arising from the ventricles, viz., in the pulmonary artery and the aorta. These valves called pulmonary and aortic are often spoken of as the semi-lunar valves. No valves are found guarding the entrance of the vessels into the auricles.

In order that we may understand the function of these valves, which play such an important part in the physiology of the heart, it is necessary that we should briefly detail the course which the blood takes from the time it enters the right auricle until it completes the round of the circulation and finds itself at the auricle again.

The venous blood flowing into the right auricle by means of the anterior and posterior vena cava, passes from this through the tricuspid valve into the right ventricle; from here it passes to the lungs by means of the pulmonary artery, where having been exposed to the action of the air and becoming greatly changed in its composition, it returns to the heart by means of the pulmonary veins, emptying itself into the left auricle, passing from here through the auriculo-ventricular opening into the left ventricle, and from thence into the aorta to be pumped all over the body to which it is distributed by means of the arteries and capillaries; it is then collected by the veins, and eventually brought back to the heart to undergo afresh its distribution to lungs and body. The use of the valves is to allow of the transference of blood from auricle to ventricle, and from the ventricles to the aorta and pulmonary artery without any chance of regurgitation.

The heart occupies a position in the middle line of the chest, being suspended from the spine by its aortic vessels.

Its base is uppermost, its apex nearly touches the sternum, and it occupies a position corresponding to the third, fourth, fifth, and sixth ribs; it is between the fifth and sixth ribs, just at their sternal insertion, where the impulse of the heart may be felt in the horse. Its other relations are with the diaphragm which is some five or six inches behind it, but with which it has no connection. On its right side is the right lung, and on its left part of the left lung. There is a triangular notch in the left lung of the horse which exposes the left ventricle, and allows it to make its impulse felt against the chest wall. The anterior face of the heart is formed by the right auricle and ventricle, the posterior by the left auricle and ventricle.

The heart, though an involuntary muscle, does not conform histologically with the involuntary muscular fibre met with in other parts of the body. It is red in appearance, its fibres are short, striated, possess no sarcolemma, freely anastomose, and contain a nucleus. The network formed by the fibres of the heart is a most distinctive feature. In some animals, sheep and ox in particular, cells of a peculiar kind are found beneath the endocardium, they are polyhedral in shape, containing protoplasm and a nucleus, and are surrounded by striated fibres. They are called the cells of Purkinje.

The arrangement of the fibres of the heart is peculiar; those of the auricle are quite distinct from the ventricle, and both are arranged in layers. Two layers have been described in the auricle, transverse and longitudinal, with circular fibres around the entrance of the veins, whilst in the ventricle no less than seven layers have been described. Owing to the peculiar direction in which these run a somewhat spiral arrangement results, but this is not fully accepted.

The heart is lined by the endocardium which is reflected over the valves. The lining membrane of the left auricle of the horse is naturally of a peculiar gray colour.

Certain fibrous rings are found in the heart where the valves are situated, and to which these obtain a firm attach-

ment. The ring surrounding the aortic opening in the ox has constantly in its substance one or more pieces of bony tissue; this is also common in the horse.

The auriculo-ventricular valves are made up of fibrous and elastic membrane, in which a small proportion of muscular fibre is found close to the attached border. The mitral or bicuspid valve in the horse consists of one large distinct segment, and several smaller ones united to form a second. The tricuspid consists of three segments, one much larger than the others being placed opposite to that portion of the ventricle leading up to the pulmonary artery.

All the valves are held in position by large and small tendinous cords composed of fibrous tissue, which cords are inserted into large muscular eminences found on the internal surface of the ventricle; the cords from one eminence do not all pass to one segment of the valve, but to two or three. Their function is to restrain the valves from passing into the auricle during the contraction of the ventricle. Other bands pass from one side of the ventricle to the opposite wall; they are called moderator bands, and their function is to restrain the ventricular wall from undue dilatation.

Both the mitral and tricuspid valves meet in the most perfect apposition when the ventricle contracts, and nothing can escape upwards into the auricle. This may be readily demonstrated in the dead heart by tying the aorta and pulmonary veins, and introducing into the left auricle a tube which admits of a powerful jet of water; the left side of the heart distends and hardens, and at last water forces its way out of the side of the vessel or hole in the auricle in which the tube is inserted. If we now open the auricle, we find the ventricle cut off from view by a tense membranous dome, convex towards the auricle, which is the mitral valve in position; not a drop of water will escape from the ventricle, though the heart be turned upside down, and it requires some little force to depress the valves. The appearance is a very pretty and singular

one, and is exactly represented in Fig. 261 of Chauveau's 'Anatomy,' first edition.

The semi-lunar or sigmoid valves, which guard the entrance into the aorta and pulmonary artery, are composed of fibrous and elastic material, and possess at the centre of each segment a small hard body, corpus Arantii, which is particularly marked in the aorta.

Owing to the arrangement of the muscular fibres of the heart, we find that the auricles and ventricles are capable of acting quite independently of each other; the two auricles contract, and then the two ventricles. The contraction of either auricle or ventricle is spoken of as its **systole**, whilst the dilatation is described as its **diastole**. We observe that when the two auricles are in a condition of diastole the two ventricles are in one of systole. Where death is caused from bleeding, we find that the two ventricles cease beating before the auricles, and the auricular portion of the right auricle acts longer than the left auricle.

A **Cardiac Revolution** or **Cardiac Cycle**, is the term used to describe the changes which occur in the heart during the time which elapses between one contraction or dilatation of the auricle and the one which immediately succeeds it. We observe that the auricles are filling with blood, which pours into them by the venæ cavæ and pulmonary veins, owing to the fact that the pressure within the auricles is lower than that in the bloodvessels, and also because the efforts of inspiration favour an aspiratory effect, due to the dilatation of the walls of the heart producing a sucking action in the auricles, and so helping to fill them. The auricles being full of blood the cavities contract, the mouths of the vessels opening into them also contract owing to the circular muscular fibres in their coats, and so produce a slight stagnation of blood in these veins and a distinct regurgitation in the anterior cava, which can be readily seen at the root of the neck of most horses. Systole of the auricle follows, the blood being driven into the ventricles which have been partly filling during the

time the blood was being collected in the auricles; as the ventricles fill their valves float up into position, the chordæ tendinæ are rendered tense, and the ventricle contracts by a peculiar wringing movement produced by the arrangement of its fibres. The blood now presses against the auriculo-ventricular valves, closing them more firmly, and as the walls contract the imprisoned blood is forced up into the aorta and pulmonary artery, pressing open the valves situated here owing to the difference in pressure between the blood in the ventricles and that already in these vessels. During this process of ventricular contraction a sound is produced, occasioned by the muscular contraction of the walls, and probably by the vibration of the tricuspid and mitral valves. Neither ventricle completely empties itself during contraction (Colin).

The blood now rushes into the aorta and pulmonary artery, but soon the pressure in the ventricle becomes negative, viz., lower than that in these vessels, and at the same time the elastic resistance of these arteries being brought into play, the blood has a tendency to regurgitate towards the ventricles and by so doing closes firmly the semi-lunar valves, a sharp sound being produced at this moment by their closure. While the ventricle is contracting the auricle is dilating, and so soon as the semi-lunar valves are closed there is a pause in the movement of the heart, during which period the auricles and ventricles are relaxed and blood is flowing into them; at the end of the pause the auricles contract and the whole process is repeated.

We have thus the contraction of the auricles, the contraction of the ventricles, and the pause. The periods these occupy have been determined for the horse, by Chauveau and Marey, by means of a cardiac sound. The value of the periods is as follows: auricular systole, two-tenths of a second, ventricular systole, four-tenths, and pause, four-tenths of a second. The duration of the ventricular systole always remains the same, viz, four-tenths of a second, no matter how fast the heart is beating, so that the frequency depends not on the time occupied in the con-

traction of the heart, but the length of the pause (B. Sanderson).

While these changes are occurring in the cavities of the heart, the organ itself undergoes some distinct changes in shape and movement as the result of them. During systole the heart becomes narrower from side to side, but increased in width from front to rear; it is reduced in all its diameters excepting its vertical one, and the reduction of its horizontal diameter assists materially in closing the auricular ventricular valves. It also alters in shape; during the period of diastole it is an oblique cone with an elliptical base; during systole it is an upright cone with a rounded base. This change in shape is accompanied by a rotation of the heart to the right, and a tilting of the apex to the left (Hermann).

This tilting outwards of the heart, due to the spiral arrangement of its fibres, may assist in producing the impulse against the chest wall, which in the horse occurs between the fifth and sixth ribs. Colin insists that in the horse the impulse is not given by the apex alone, but by the lower half of the wall of the left ventricle. Experiments made on some animals prove that the apex does not leave the chest wall, but that the impulse is due to the hardening of the ventricular wall in contact with the chest wall. This impulse against the chest agrees with the closure of the auriculo-ventricular valves, and the bursting open of the sigmoid valves (Sanderson). In the horse the apex does not rest on the ribs, but is free and directed towards the sternum.

The action of the valves of the heart during a cardiac cycle is peculiar and interesting. We have described how the auriculo-ventricular curtains are floated up as the ventricle fills, and how with increased pressure they come together, being prevented by the chordæ tendinæ from being carried too far; we have also noticed how the reduction in the horizontal diameter of the heart assists the action of these valves; further, experimental inquiry has determined that when the ventricular systole is at its height these valves bulge upwards into the auricles,

assuming a concave surface towards the ventricle. This appears to be only the case in the horse, and the information is obtained by the researches of Chauveau and Colin. The pulmonary valves, and probably the aortic, meet not only at their free border but actually overlap. Chauveau states that he has tried experimentally to hold back one of the pulmonary valves, but the others have applied themselves so closely around the finger that it was impossible to produce a patent opening. In the aorta it is probable that overlapping does not occur to the same extent, and here the the corpora Arantii are of value. When these valves are not acting they lie towards the wall of the vessel, but do not in the aorta, as was at one time considered, cover the openings of the coronary arteries.

The elastic recoil of the aorta does not exercise its entire pressure upon the valves, for we observe that the diameter of the aorta at its origin is greater than the aortic opening from the ventricle, and so the muscular substance of the heart bears largely the shock of recoil.

The **Cardiac Sounds** are really four in number, but as they are in pairs we recognise only two. The first sound is a long one, due to the vibration of the auriculo-ventricular valves and the muscle sound of the contracting ventricle. The second sound is due to the closing of the semi-lunar valves of the aorta and pulmonary artery; it is a short sound. The two sounds are reproduced by the words '*lubb, dŭpp.*'

Various instruments have been designed for the purpose of displaying in a graphic manner the movements of the heart, both internal and external. The internal movements are ascertained by means of an instrument termed a cardiac sound, first used by Chauveau and Marey. It is a tube containing two hollow balls; the air in these is compressed when the cavities contract, and the compression moves a lever placed in connection with the tube. The instrument is passed into the right heart through the jugular vein, and into the left ventricle through the carotid. Burdon Sanderson states that it causes no inconvenience to

the animal, due to the fact that no sentient nerves are supplied to the lining membrane of the bloodvessels or even to the heart. It is doubtful to my mind whether tracings produced by this means are completely trustworthy, for the presence of these two air-bags in the heart must interfere to an extent with its normal function; for example, the experiment on p. 52 gives a pulse of sixty to the minute for the horse, which is distinctly abnormal.

A tracing obtained from the heart of the horse is shown in Fig. 1; each vertical line represents one-tenth of a

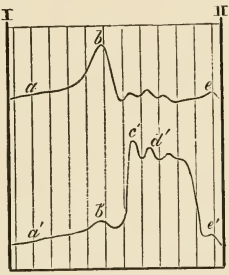


Fig. 1.—Simultaneous Tracings from the Right Auricle and Ventricle of the Horse, after Chauveau and Marey (Foster).

The auricular curve is *a*, *b*, *e*, the ventricular curve *a'*, *b'*, *c'*, *d'*, *e'*. *b*, the contracting auricle which at once relaxes, and is followed by the sudden upstroke in the lower curve terminating at *c'*, indicating the sharp contraction of the ventricle, which is maintained with certain oscillations for about three-tenths of a second, and then suddenly relaxes; the pause follows, a part of which may be seen at *a* and *a'*.

second; the curves do not indicate the force of the stroke, but only the intra-cardiac pressure. It is seen from the diagram that the auricles contract first, followed by the ventricles; the former is slower and shorter than the ventricular systole, which is sudden, maintained for some time, and then rapidly falls. During the ventricular systole the heart makes its impulse against the chest wall.

The impulse of the heart against the chest wall is obtained by means of the cardiograph, of which there are

many forms. Their essential construction consists of a button which is pressed upon by each impulse of the heart, and conveys the movement to an elastic air-chamber, which transmits it to a recording lever. By this means we get a graphic representation of the heart's impulse.

The cardiograph demonstrates that the aortic valves close slightly before the pulmonary.

Capacity of Heart.—The quantity of blood in the heart can only be ascertained approximately; measuring the capacity of the chambers is no guide. Munk states that the capacity of the ventricle in a horse weighing 880 lbs. is about 1·76 pints, equivalent to 2·35 lbs. of blood; each ventricle contains one-thirtieth of the total blood, so that when both contract one-fifteenth of the total blood is ejected (M'Kendrick). My own observations on the capacity of the heart have not as yet enabled me to make any general statement.

Colin gives the capacity of the left ventricle of the horse at 1·76 pints, and states that at each systole two-thirds or three-fourths of this quantity is injected into the aorta, viz., 1·172 pints to 1·364 pints; the left ventricle at each contraction, according to this observer, forces into the aorta about one-twenty-fifth of the total blood of the body.

Colin gives the following table of capacities of right and left ventricle:

	Right Ventricle.	*Left Ventricle.*
	Pints.	Pints.
Small horse - -	1·42	1·29
Medium size horse -	1·76	1·23
Big horse - -	3·34	2·36

This is only a part of the table, the figures of which are found to vary widely. Measuring the capacity of the heart is therefore fallacious, for in the above table each side of the organ should have held the same quantity of blood.

Intra-cardiac Pressure.—Though both ventricles deliver the same amount of blood, the pressure in each cavity is different. Chauveau puts the systolic pressure in the left

ventricle of the horse as equal to a column of blood 5·35 feet in height: in the right ventricle as equal to one 1·04 feet in height. According to Colin's experiments, made with a manometer in the form of a long tube, the left ventricle is capable of sustaining a column of blood 6·56 feet high, whilst the force in the right ventricle will support in the pulmonary artery a column of blood 1·64 feet high. This, calculated on the surface of the ventricle, is equal to a force of 72·6 lbs. for the right ventricle, and 290·4 lbs. for the left (Colin). The right ventricle does about one-fourth less work than the left. Munk gives the daily work of the heart of the horse as equal to one-thirty-sixth of a horse-power, or nearly 15·3 lbs. lifted one foot high per second.

The term **Blood Pressure** is frequently used in the physiology of the circulatory system. It is one we shall have to consider in detail when we come to speak of the blood-vessels; but we should clearly understand that the condition is due to the amount of blood pumped into the vessels by the heart, and this amount will depend principally on the rate at which that which is in front of it in the vessels escapes into the veins. If the arterioles are contracted so that the amount passing into the veins is reduced in quantity, then a larger bulk of blood will be between the pump and its outlets, and the blood pressure rises; if, on the other hand, the blood is passing rapidly through its extensive arterioles into the veins the blood pressure falls. When the amount poured into the venous system in any given time, is equivalent to that pumped into the arterial system during the same time (which is the perfectly normal condition), we speak of the pressure as being a constant one.

The above facts may be tabulated as follows:

When the heart is more active the blood pressure rises.
„ „ less „ „ „ falls.
When the arterioles contract the blood pressure rises.
„ „ dilate „ „ falls.

Nervous Mechanism.—The heart possesses no sensory nerves; it may be handled, pinched, pricked, or otherwise

injured without provoking the least sign of pain on the part of the animal. Colin's experiments in this direction on horses are most conclusive. Not only is the external surface insensible to pain, but the internal surface also. The experimental introduction of foreign bodies into the cavities of the heart produces no pain. This fact has been previously mentioned when speaking of the cardiac sound.

These results are confirmed by what we know of pathological processes; those foreign bodies found so commonly in the heart of the cow are remarkable for the fact that they produce no suffering, though great disturbance of the circulation occurs.

The nerves supplying the heart are the pneumogastric and sympathetic. The latter has very extensive connections with various ganglia before it reaches the heart. The function of these two nerves is diametrically opposite. Whilst one, the pneumogastric, has a controlling, or, as it is termed, an inhibitory effect over the movement of the heart, the sympathetic has an accelerating or augmenting effect. Histologically the two nerves differ greatly in structure, the pneumogastric being a medullated, whilst the sympathetic is a non-medullated nerve.

If the vagus nerve in the neck be gently excited, the heart's beats are reduced in *force* and *frequency*; if strongly stimulated, the heart stops in diastole. If the nerve be divided the heart beats more rapidly, for now the inhibitory power over the sympathetic is lost, and the latter has it all its own way. When the cut end of the pneumogastric is stimulated we restore to an extent the inhibitory power, and the heart's beats become fewer and more feeble. If the spinal cord and both sympathetics be divided, the inhibitory power over the heart produced by the vagus is intensified, owing to the loss of its antagonistic nerve, and the result is that even feeble stimulation of its fibres arrests the action of the heart.

The sympathetic is the augmenting or accelerating nerve of the heart; and as such is the antagonist of the vagus.

Section of the sympathetic reduces the number of beats of the heart, and, as we might expect, stimulation of the cut end causes the heart to beat with increased rapidity.

Both the pneumogastric and sympathetic have a central origin in the medulla, but in addition the sympathetic has extensive connection with the spinal cord. We have, therefore, in the medulla an inhibitory and augmenting centre; these are both differently affected by the gases brought to them by the blood. CO_2 in large quantities excites the inhibitory centre, whilst oxygen stimulates the augmenting centre. The inhibitory or controlling centre is in the constant exercise of its function throughout the whole life of the animal; this is not the case with the augmenting or accelerating centre.

The inhibitory action of the vagus may be excited by reflex impressions conveyed to the medulla—for instance, fainting through shock or through blows on the abdomen, are instances of impressions conveyed to the medulla exciting the cardio-inhibitory centre.

The fibres conveying inhibition to the heart from the centre in the medulla are in company with the spinal accessory, for if these be divided, stimulation of the vagi has no action on the heart.

If the vagus of an animal be stimulated during the experiment of graphically recording the blood pressure, it is found that almost immediately after the stimulation the blood pressure falls, the curve being a sudden one; when the current is shut off, the beats of the heart return, and the pressure rises rapidly until the normal condition is obtained.

Contrary to what might be imagined, repeated excitation of the vagus, when reaction sets in after withdrawing the current, rather increases than decreases the force of the contraction; and, on the other hand, repeated stimulation of the sympathetic is followed in the reactionary period by a weakening of the heart's beats.

Gaskell does not regard either the cardiac ganglia or the nerves supplying the heart as the cause of the beat of the

heart, but rather that this is due to changes taking place in the muscle itself; and he calls especial attention to the cellular and protoplasmic features of the heart's muscle in support of this statement, likening the contraction of cardiac muscle to the spontaneous movements of undifferentiated primordial protoplasm.

When life is suddenly destroyed in horses by shooting through the head, it is not uncommon for the heart to continue beating for one or two minutes. Colin divided the spinal cord in a horse and established artificial respiration, fifteen minutes after the operation the heart was beating 42 to the minute, and it did not cease contracting for 50 minutes after the section. In another case the cord and both pneumogastrics and sympathetics were divided: artificial respiration being established the heart beat for 24 minutes. In a third experiment the animal was decapitated and both carotids tied; artificial respiration being established the ventricles contracted for 17 minutes, and the auricles for 34 minutes.

Ganglia are found in the heart—in the frog two are well defined, known as Remak's and Bidder's ganglia. In mammals ganglia are found in the venæ cavæ and pulmonary veins, also in the walls of the auricles, auriculo-ventricular groove, and in the base of the ventricles. The auricular septum in its central parts is free from ganglia (Foster). The cardiac nerves, viz., the vagus and fibres from the sympathetic, form plexuses around the aorta. One of the theories of the cause of left laryngeal paralysis in horses, is that based on the anatomical position of the left recurrent nerve relative to the aortic trunk and bronchial glands. Aortic compression and bronchial glandular enlargement are the assigned causes of the muscular atrophy of the larynx.

The right vagus nerve is said to have more influence over the heart than the left.

It would be outside the scope of this work to enter more fully into the nervous mechanism of the heart, particularly that dealing with the nature and causes of contraction, but

in conclusion we must briefly notice the results of Gaskell's profoundly philosophic work in this direction. According to this authority the vagus is the trophic nerve of the heart; it excites processes of repair (anabolism), builds up the muscular tissue, and is, in fact, the nutrient nerve to this organ; the sympathetic, on the other hand, excites processes of decomposition or destruction (katabolism), in just the same way as a motor nerve passing to muscle excites katabolic processes in the muscle elements as the result of work. If we carefully consider this theory in conjunction with what we have previously stated respecting the opposite action of the vagus and sympathetic, we can see that it receives every support.

CHAPTER IV.

THE BLOODVESSELS.

Mechanics of the Circulation.*—The laws which regulate the flow of fluids through elastic tubes apply with equal force to the bloodvessels.

An elastic tube converts an intermittent flow into a constant one; this it is enabled to do by the recoil of its coats following on previous distension. The effect, however, of the elastic reaction of the walls of the vessel is to diminish the rate of flow, though at the same time it increases the amount of fluid discharged.

Applying these principles to the circulation, we can readily see their important bearing in the body, and appreciate the considerable economy effected in the work of the heart through the blood being pumped into elastic rather than rigid tubes.

In a rigid tube as much fluid as is pumped in at one end issues at the other, and the same will hold true for elastic tubes unless they offer resistance to the flow. The effect of peripheral resistance is to convert an intermittent into a continuous flow.

In the bloodvessels, the capillaries and smallest arteries, from their small size and considerable area, offer great resistance to the flow of blood through the arteries; this causes the arteries to be distended, and the elastic recoil of the stretched walls leads to the continuous flow through them in spite of the intermittent action of the heart.

The pressure exerted on the wall of a tube diminishes the

* 'Physiological Physics,' by M'Gregor-Robertson, has helped me considerably with the mechanics of the circulation.

further the tube is removed from the central pump; this mechanical law applies to elastic as well as rigid tubes; but as applied to the bloodvessels, we find that instead of there being a gradual reduction in pressure, the latter decreases irregularly owing to the force being used up in overcoming the peripheral resistance. In arteries, for example, the pressure diminishes slowly; in capillaries, owing to the increased resistance, the reduction is very rapid, whilst in the veins it decreases slowly.

The velocity of flow is inversely as the sectional area of the tubes; the total sectional area of the capillaries is greater (about 500 times) than that of the aorta, therefore the velocity is reduced; from the capillaries to the heart the area becomes smaller and the velocity increases. The narrower the vascular bed the more rapid the flow, the wider the bed the slower the flow.

If fluid be forced into an elastic tube, and the flow maintained under constant pressure, the fluid will behave as if being forced through a rigid tube; but if the pressure be rendered an inconstant one, the elastic walls distend at the increase of pressure and recoil when the pressure is reduced; this distension and recoil occurs throughout the whole length of the tube, and produces a wave which we term in living tubes the pulse. We must be careful to avoid the error of considering that this wave represents the flow of blood in the vessel, it does not; it is simply the outcome of an impression at one end of the tube, which is travelling very much faster *along the walls* of the tube than the blood which is within.

The rate at which the wave travels depends on the elasticity of the walls: the more elastic the tube the slower the wave and the greater its height; the more rigid the tube the faster the wave and the less its height.

By an application of these physical principles to the living body, we are able to account for many of the physiological problems of the circulation in bloodvessels; the intermittent action of the heart, the elastic walls of the arteries, the peripheral resistance, the increase in the width of the

bed of the vessels from the heart to the capillaries, and the decrease in width from the capillaries to the heart, account for the high blood pressure in the aorta, rapid flow of blood and throbbing in the arteries, the slower flow and lower pressure in the capillaries, and the pulseless flow and low pressure in the veins.

We have noted that the pressure of the blood is highest in the arteries and least in the veins; it is this difference in blood pressure which is the cause of the circulation; if the pressure were the same throughout the whole circulatory system there would be no movement of blood, for the latter naturally moves from the higher to the lower pressure.

By **Blood Pressure** we understand the actual pressure

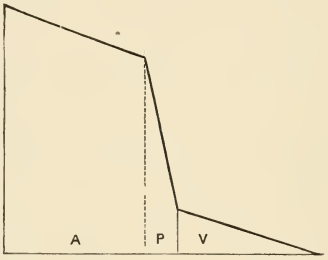


FIG. 2.—DIAGRAM OF BLOOD PRESSURE.

A, Arteries. P, Peripheral Region (minute arteries, capillaries, and veins). V, Veins (Foster).

exerted by the blood on the walls of the vessel due to the action of the heart; this pressure can be measured by suitable instruments, and is found to be in the carotid of the horse from 8·88 feet to 13·53 feet of blood—that is, the pressure in the vessel is capable of supporting a column of blood from 9 to 13 feet in height. The pressure is constantly varying, it increases with the contraction of the ventricle and falls with its relaxation, it increases with expiration and falls at inspiration.

As we pass from the aorta to the capillaries the blood pressure becomes gradually reduced; in the capillaries the

reduction is sudden, and in the veins the pressure is very low (see Fig. 2).

In the carotid of the rabbit the pressure is equivalent to 3 feet of blood; in the capillaries it has fallen to 10 or 15 inches, and in the veins to 1½ to 2 inches only. It is possible for the blood pressure to be negative; such is observed in the great veins opening into the heart and also in the auricles, the negative pressure being produced by the act of inspiration; by its presence the flow of blood into the heart is facilitated.

The blood pressure in the veins is from one-twentieth to one-tenth of that in the corresponding arteries; these results have been obtained on vessels near the heart. The greater distance the veins are from the heart the greater the pressure. M'Kendrick states that experiment has shown the blood pressure in the external facial vein of the sheep to be 15 inches, in the brachial 2 inches, and in the crural vein 5·8 inches of blood.

Capillary pressure is very difficult to ascertain. Du Bois Reymond calculates it as being one-half that in the large arteries; it is probable that in many places it is much less than this.

The larger undulations obtained in blood-pressure experiments are not all variations in pressure due to the heart-beat, but largely in part to the respiratory movements, the expiratory effort having on the whole the effect of reducing the pressure in the vessels, whilst, conversely, inspiration raises the pressure within them.

The conditions affecting the rise and fall of blood pressure have been dealt with on p. 57; we have here only to notice the effect of blood-letting upon it. Blood pressure, contrary to what we might anticipate, is not affected until two-fifths of the blood in the body have been removed.

We have described the recoil of the bloodvessel following on distension. This elastic recoil produces what is known as **Tension**, between which and blood pressure a clear distinction must be drawn. Blood pressure is the pressure of the blood on the coats of a vessel, whereas tension is the

pressure of the coats of the vessel on the blood. The term 'tension' is one in constant use in pathology; pulses of high and low tension are frequent accompaniments of disease, and methods of measuring them have been known for some time past. The simplest description of the apparatus for registering the movements of a vessel is that it is a delicate lever placed on the artery, the excursions of which are registered on a piece of paper which travels past the end of the lever. Such a tracing is represented in Fig. 3, from the human carotid artery.

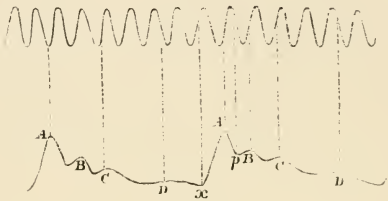


FIG. 3.

The up-stroke x A, in the second tracing, is due to the contraction of the ventricle; from A to x, in the first tracing, the blood is flowing from the peripheral arteries to the capillaries; the descent of the lever is here broken by several irregularities. The first one, p, in the second tracing, is termed the first tidal or predicrotic notch; the second notch in front of C is the aortic notch; the elevation, C, is the dicrotic or recoil wave, and is due to the closure of the aortic valves, and the elevation, D, is the post-dicrotic wave. The curve above is that of a tuning-fork with ten double vibrations in a second (Foster, after Moens).

With the exception of the aortic notch, physiologists are not agreed as to the cause of the other irregularities in the down-stroke. The dicrotic wave is often of considerable practical importance, giving a double beat to the pulse on each single contraction of the heart.

The instrument which records these movements, and is known as the sphygmograph, does not register blood pressure, it simply registers the expansion and collapse of the tube at the moment the wave is passing along the vessels; it is not a representation of the wave itself. In examining a pulse-

tracing we judge of the tension of an artery by the height of the up-stroke. In a pulse of high tension the vessel is so full that it can hold but little more; the upstroke is therefore a short one, whilst the down-stroke is very oblique. In a pulse of low tension the up-stroke is nearly vertical and high, the down-stroke oblique; the vessel not being very full is capable of holding much more fluid, and its movements are correspondingly affected.

The **Pulse** is due to the wave movement set up in the vessels, as the result of the aorta being suddenly distended by the contraction of the left ventricle; this wave movement is very much more rapid than the progress of the blood itself. The pulse-wave is about 18 feet in length, and travels at the rate of from 15 to 30 feet a second, whilst the velocity of the blood, even in the large arteries, is not greater than 1½ feet per second. Owing to the length of the pulse-wave, the beginning of it is lost in the small arteries and capillaries before the end of it has left the aorta (Foster).

The pulse will vary in character depending upon age, condition, height of body, and state of the system; it also differs according to the animal. Colin gives the following table of pulse-rate in different animals:

Elephant	-	25 to	28	beats per	minute.
Camel	-	28 „	32	„	„
Horse	-	36 „	40	„	„
Ox	-	45 „	50	„	„
Sheep	-	70 „	80	„	„
Pig	-	70 „	80	„	„
Dog	-	90 „	100	„	„

The pulse is much quicker in the young animal than in the adult, that of a foal at birth beating 100 to 120 per minute, and of a calf 92 to 132 per minute;* in old age the pulsations become reduced, and the artery much weaker. As a rule, the higher or bigger the animal the lower the

* Colin.

pulse rate. The more rapid the pulse, the greater the quantity of blood in circulation.

The **Velocity of the Blood** varies in the arteries, capillaries, and veins, being greatest in the former, least in the capillaries, and rising again in the veins. The velocity of blood-flow is due to the width of the bed formed by the vessels; as the arterial system expands, the velocity diminishes. In passing through the capillaries, with their immense network, the velocity is at a minimum; in passing towards the heart the vessels are reduced in number, hence the bed is less, and the velocity accordingly increases. The cause of the flow throughout the entire system is the contraction of the left ventricle, aided by certain accessory movements, which will shortly be alluded to. The velocity does not depend upon the blood pressure, but upon the force of the heart and the peripheral resistance.

The vascular system has been compared to two cones placed base to base, the apex of one being the left ventricle, of the other the right auricle; where the bases of the two cones meet is the capillary network; the sectional area of this has been estimated as 500 times greater than that of the aorta, whilst the passage of blood through it, owing to the resistance experienced, is 500 times slower than in the aorta (Volkmann).

According to the same authority, the velocity of blood in the carotid of the horse is from 11·8 inches to 15·75 inches per second; in the metatarsal artery of the horse 2·2 inches per second; and in the jugular vein 8·85 inches per second. Chauveau found in the great arteries near the heart a velocity of 20·47 inches per second during systole; at the beginning of diastole 8·66 inches per second, and during the pause 5·9 inches per second (M'Kendrick).

The velocity of the blood is increased by each systole of the ventricle, and in arteries by each expiration; inspiration, on the other hand, does not retard the flow of blood in the thick-walled, highly-distended arteries, but assists it in the veins. The velocity of the blood is greater in the pulmonary than in the systemic capillaries, while the

velocity in the venæ cavæ is half that in the aorta (Landois and Stirling).

The **Duration of the Circulation** depends upon the length of time which it takes a red corpuscle to travel from a given point and back to it again. In the horse the complete circuit is performed in 31·5 seconds (Vierordt), and is equivalent, according to the latter observer, to about 27 beats of the heart: this would give a pulse of 51 for the horse, which is decidedly abnormal. According to Munk, an amount of blood equal to that in the body passes through the heart of a horse in fifty seconds, and of an ox in forty seconds (M'Kendrick). The blood-cell spends most of its time in the capillaries of the tissues and lungs.

The volume of an organ depends upon the amount of blood in it. This is well exemplified in certain pathological conditions, such as engorgements of the spleen, where the organ may be as much as ten times its normal size. Physiologically we see the same fact demonstrated in erection of the penis.

We must now glance at the circulation through the various systems of the body, and the methods by which it is assisted.

Arterial Circulation.—The walls of the arteries are both elastic and muscular; the former condition is predominant in the large arteries of the body, where an elastic resistance is necessary to provide for the extra bulk of fluid sent out at each contraction of the left ventricle, and where, in addition, the elastic recoil of the vessel converts an intermittent into a continuous flow: the smaller vessels, on the contrary, are principally muscular, for they act as a tap, and regulate the blood supply to the part through the aid of certain nerves known as vaso-motor.

We have previously drawn particular attention to the fact that the pulsations in an artery represent a wave resulting from the expansion and contraction of the larger arterial walls, which movement travels very much faster than the blood itself, but does not represent the progress of the fluid in the tube.

The **Capillary** circulation is readily observed microscopically in the web of the frog's foot. The velocity of blood through the capillaries depends upon their size; in some vessels the red cells may be seen rushing along the centre of the tube, whilst the white ones course leisurely along the side, exhibiting a tendency to adhere together, a phenomenon which is not observed in the red cells of the circulating blood; where the capillary vessels are very small the cells only pass through one abreast, and the rate of the current is reduced.

The walls of the capillaries are elastic, and by this means they readily distend or recoil, and by so doing accommodate themselves to the increase or decrease in the blood supply to the part.

The **Venous Circulation.**—The contraction of the left ventricle is sufficient to drive the blood all over the body, but in the veins this force is assisted by the muscles compressing the vessels, by the presence of valves which prevent regurgitation, (especially in the veins of the limbs where the fluid has to ascend against gravity), and, lastly, the circulation is assisted in the larger veins by the process of inspiration and the dilatation of the right auricle, both of which have an aspirating effect on the blood in the larger veins. The sucking action of the left auricle assists also in drawing the blood in the pulmonary veins towards the heart.

Veins are normally pulseless, but an exception must be made to this statement in the case of the lower extremity of the jugulars, just where they enter the chest. It is quite common in the horse to observe pulsations in these vessels for an inch or so up them, due no doubt to the action of the tricuspid valve. It is, however, distinctly abnormal for these venous pulsations to extend any distance up the neck, for then it indicates insufficient closure of the tricuspid, due to a debilitated state of the system or actual disease of the valve itself, which latter in the horse is a very rare condition.

There are certain veins where no valves exist—for

instance, in the sinuses of the brain and in the veins of the foot; in the latter case the movements occurring in the wall, the result of expansion and contraction, are amply sufficient to assist in the immense venous circulation of the part.

Influence of the Nervous System.—When a part requires more blood—for example, an actively secreting gland—the vessels leading to it dilate; when the necessity for the increase has passed, the vessels contract. This dilatation and contraction of the bloodvessels is under the control of the nervous system, through the minute nerves known as vaso-motor distributed to the muscular walls of the small arteries, and it is possible that the branches of nerve which dilate the vessels are not those which constrict them.

The nerves which contract the vessels are called vaso-constrictor, whilst those which dilate the vessels are called vaso-dilator; it is believed that in most cases dilatation of the vessels is due to diminished constricting influences, rather than to special dilator fibres.

If the sympathetic nerve in the neck of a horse be divided, the temperature of the face and neck on the same side rises, the skin becomes congested and sweating occurs. In other words, the system of nerves which constrict the bloodvessels is paralysed by division, and dilatation results. If now the cut end of the nerve be irritated, the temperature of the part falls, the skin congestion is removed, and sweating ceases; the constrictor fibres are now active, and the amount of blood sent to the part is considerably reduced.

The above experiment is best made on the rabbit, where the vessels may be seen dilating and the skin reddening.

The vaso-motor fibres may run in a sympathetic or a spinal nerve. The sciatic nerve, for example, contains the vaso-motor fibres for the posterior extremity, whilst the sympathetic system contains similar fibres for the abdominal viscera. It is said that the vaso-dilator nerves are principally derived from the cerebro-spinal system, whilst the constrictors belong to the sympathetic.

Experiment has shown that the vaso-motor nerves over the whole body are under the control of a vaso-motor centre in the medulla; certain centres exist in the spinal cord, but these are subordinate to the centre in the medulla. By means of impulses passing out from this centre, the whole of the vessels of the body are kept under control, dilated or contracted as needful, and in this way vascular tone is maintained.

If the vessels of a part be cut off from the vaso-motor centre in the medulla, relaxation occurs through paralysis of their muscular coat, and dilatation follows.

The vaso-motor centre in the medulla is situated in the floor of the fourth ventricle; it is readily affected by the quality and character of the blood circulating through it —for example, an increased venous condition of the blood leads to contraction of the smaller arterioles; this constriction means a considerable opposition to the flow through the arteries, as the result of which the blood pressure is raised. The rise and fall in blood pressure is largely under the control of this centre, through the resistance or otherwise offered to the flow of blood through the periphery. Stimulation of the vaso-motor centre means a constriction of the smaller vessels, but it is possible for the opposite condition to be brought about, viz., inhibition of the centre, in which case vascular dilatation occurs. This is more brought home to us clinically than physiologically. The engorgement of the spleen, portal system, etc., seen in certain diseases, must largely be due to inhibition of the vaso-motor centre, and a fall in blood pressure due to the dilatation of the vessels.

In the rabbit this can be experimentally produced through a nerve termed the depressor, which is in connection with the pneumogastric, and runs from the heart; if the central end of this nerve be stimulated, though the heart-beats remain unchanged, the blood pressure slowly falls, owing to the dilatation of the abdominal vessels due to the inhibition of the vaso-motor centre in the medulla.

Besides the vaso-motor centre in the brain, and the subsi-

diary ones in the spinal cord, there is reason to believe that local centres exist which, so long as they are in connection with the medulla, are subordinate to it, but may, when separated from it, act as centres on their own account; this latter condition being abnormal, it is probable that the local centres are for the purpose of keeping up a closer touch with those in the cord and medulla, and so maintaining the normal vascular tone.

Peculiarities in the circulation through various parts occur as the result of their special function; they are observed in the brain, erectile tissues, etc. The great vascularity of the brain necessitates that the blood should pass to it with a degree of uniformity which will ensure the carrying out of its functions. We see this provided for in the frequent arterial anastomoses—for example, the Circle of Willis and the Rete Mirabile of ruminants, which ensures that not only does the blood enter with diminished velocity, but that if a temporary obstruction occurs in one vessel its work is readily performed by the others. The rete mirabile alluded to, which forms the beautiful arterial plexus on the base of the brain of ruminants, is considered by some to regulate the flow of blood to the brain while the head is depressed during grazing, and that it accounts for the absence of cerebral hæmorrhage in these animals. It is probable that this may be one of its functions; but the horse possesses no rete, and his head is depressed during grazing for more hours out of the twenty-four than is the case with ruminants. It has probably, therefore, some other function to perform.

The manner in which the vessels break up in the pia mater before entering the brain substance, is also another arrangement for equalizing the distribution of the blood. The venous arrangement of the brain is very remarkable: the walls of the veins are composed of layers of the dura mater, and even portions of the cranial bones may enter into their formation. The veins or sinuses of the brain are large cavities which, from their arrangement, are most unlikely to suffer from compression, and from the rigidity

of their walls are not capable of bulging as most veins do when obstructed; in this way the return of the venous blood is provided for.

The pulsations observed in the exposed brain are not due to the pulse in the arteries of the brain, but arise from the respiratory movements; expiration causes the brain to rise by hindering the return of blood, whilst inspiration causes it to fall by facilitating the return of blood.

The cerebral circulation is considerably assisted by the presence of fluid within the ventricle of the brain. This fluid readily passes from ventricle to ventricle, and from ventricle to spinal cord; in this way, as the external pressure becomes greater the internal becomes less, and so compression of the brain substance is avoided.

The value of these provisions in the case of draught horses with tightly-fitting collars is very evident; as a practical fact a tight collar pressing on the root of the neck rarely produces any cerebral symptoms; but this is probably due to the natural provision existing to prevent enlargement of the veins or considerable blood pressure on the brain.

The singular arrangement of the venous plexuses of the corpus cavernosum penis, admits of this organ attaining a condition which in the brain every measure is adopted to prevent—viz., a vast increase in size. The enormous size of these venous plexuses, their frequent intercommunication, the muscular pressure to which the veins leading from the sinuses are exposed, produce a considerable increase in the volume of the organ under the direction of the vaso-motor nervous system.

In some organs the vascular arrangement is peculiar, and probably depends on the function of the part. It is not clear, however, why the spermatic artery and plexus of veins should possess such a remarkably tortuous course. Doubtless, in some way or other, it is concerned with the secretion of the glands with which the vessels are connected, but its use is far from clear. On the other hand, tortuous vessels in the walls of the hollow viscera, such as the

stomach and intestines, perform a very evident function. We have only to think of the size of a collapsed and full stomach in the horse, to recognise the necessity for some arrangement existing to prevent stretching of the vessels or interference with the blood supply.

The vast venous and arterial plexuses of the foot of the horse is a peculiarity of the circulation which is dealt with in the chapter devoted to the Foot.

CHAPTER V.

THE VASCULAR GLANDS.

Under this heading are comprised certain so-called ductless glands or blood glands, of which the spleen is the representative. Their function is obscure: they secrete nothing, but they exercise a certain control over the constitution of the blood and other tissues, though in some cases even this little is unknown respecting them.

The **Spleen** does not appear absolutely essential to life; it has constantly been removed without causing death. The chief facts in connection with its function which have been ascertained, are those relating to the formation and destruction of blood corpuscles. The blood of the splenic vein contains more white cells than that of the splenic artery, hence it has been inferred that they have been formed in the spleen. The worn-out red cells of the blood appear to undergo disintegration in the spleen; more iron is obtainable from the spleen than corresponds to the amount of blood it contains, and this is supposed to result from the disintegration of the red cells.

From the intimate connection the spleen has with the stomach, and the fact that it becomes larger after a meal, it has been supposed by some to be concerned in elaborating or storing up the proteid principles of the food. Clinical experience, especially in the tropics, constantly forces on one the value of the spleen as a reservoir in those cases where the blood is driven from the surface of the skin and thrown on the viscera. After an attack of continued fever I have known the spleen contain the greater part of

the blood in a horse's body, and to require two men to lift it out of the abdomen after death.

Roy has shown that the spleen is possessed of rhythmical movements, expanding and contracting at regular intervals through the medium of the muscular fibres of the capsule, and not by means of the blood pressure, of which the circulation in the spleen is found to be independent. The muscular movement is under the control of automatic ganglia situated in the organ itself. Tizzoni asserts that new splenic structures are formed in the omentum of the horse and dog after destruction of the spleen (Landois). It is certain that when the spleen is destroyed that the lymphatic glands and red marrow of bones become, as a compensatory effect, more active in forming red blood cells.

The **Thymus** is especially active during intra-uterine existence, and for a short time after birth. It forms blood corpuscles, in this way assisting the other tissues engaged in this operation, at a time when the greatest activity is required from them—viz., during early life. The thymus disappears towards puberty; in the horse and ox at two years old. In hybernating animals it acts as a storehouse for fat.

The **Thyroid** is connected with the production of mucin in the body, for removal of this gland gives rise to myxœdema, or mucinoid degeneration of the tissues; the composition of the blood is also affected by its removal, for there is a reduction in the number of red cells and an increase in the white. Removal of the thyroid leads to a fatal cachexia. Professor Horsley, whose name is intimately connected with what is known of the functions of this body, has shown that both ruminants and horses suffer from fatal cachexia after removal of the thyroid. The function of this gland is quite obscure; it is considerably more active in intra- than in extra-uterine life.

The **Anterior Renal Capsules** have been supposed to be connected with the removal of the worn-out pigment from the body. Their function is involved in mystery.

The function of the **Pineal** and **Pituitary bodies**, though classed as blood glands, is absolutely unknown. The pineal is considered to be the remnant of an ancestral eye.

CHAPTER VI.

RESPIRATION.

The means by which the blood becomes purified by passing through the lungs must now engage our attention, but we must first glance at the mechanism of respiration.

The lungs occupy the whole cavity of the thorax; during life no space exists between the pulmonary and costal pleura, so that the case is an air-tight one. So long as this air-tight condition is maintained, any movement which tends to increase the size of the case, such as the retreat of the diaphragm and the advance of the ribs, causes a distension of the sacs and the air rushes in; by a reversed process it is pressed out, viz., by a collapse of the chest wall. If, however, the cavity of the chest be opened to the external atmosphere the lungs collapse, as the pressure within and without is the same; such a condition would lead in the horse to asphyxia, as the pleural cavities communicate; but in those animals where the right and left pleural sacs are distinct, the lung on the wounded side only would collapse.

The process by which the chest is filled with air, known as **Inspiration**, is a purely muscular act. The diaphragm, as the chief muscle of inspiration, recedes; the ribs are drawn forwards and outwards, their posterior edges everted, the intercostal space widened; by this means the capacity of the chest is increased, and air rushes into the lungs, distending them to the now increased capacity of the chest.

The increase in the size of the chest which occurs during quiet inspiration in the horse is stated by Colin to be as follows: the antero-posterior or longitudinal diameter of the chest is lengthened by 4 to 5 inches, and the transverse diameter between the eleventh and twelfth ribs increased by 1½ inches.

Only the last ten pair of ribs take, under ordinary circumstances, any share in respiration; this is due to eight true ribs being covered by the scapula; when, however, a difficulty occurs in the breathing, the elbows are turned out which brings other muscles into play as auxiliaries in respiration, and a certain number of the true ribs now assist in increasing the capacity of the chest.

The Movements of the Diaphragm during respiration are, as might be imagined from the attachments of the muscle, of a peculiar kind. The diaphragm works to and fro, not equally over its whole surface, for the central portion moves but very little owing to its connection with the posterior vena cava, and the part of the diaphragm below this vessel is so short that its movement is very limited.

The chief motion in the diaphragm lies in its upper part. At each inspiration this recedes, carrying back with it the liver, stomach, and spleen. At each expiration it advances, carrying with it the viscera which were previously displaced.

In Fig. 4 (after Sussdorf) the body is supposed to be divided horizontally. The position of the diaphragm and the displacement of the viscera during respiration are clearly seen.

Expiration.—The chest having been filled with air, the next process is its expulsion, and the mechanism here concerned is not fully agreed upon by physiologists. Whilst some hold that it is a purely non-muscular act, others contend that certain muscles do share in the process. All are agreed that the elastic reaction of the lung induces it to retract, the effect being to draw the diaphragm forward, moreover, that the elastic recoil of the cartilages of the false ribs decreases the diameter of the chest and assists

the lungs in expelling the air. The compression which the abdominal contents undergo in inspiration, causes the abdominal muscles to descend; this is now relieved, and the process of expiration is further assisted by the contraction of these muscles, which forces the viscera forward against the diaphragm.

The action of the muscles of the chest during respiration

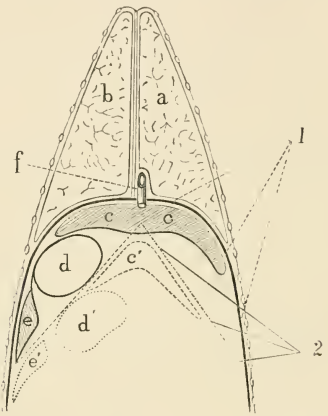


Fig. 4.—Horizontal Section of the Horse's Chest, looked at from above, illustrating the Movements of the Diaphragm.

a, right lung; *b*, left lung. 1. Position of the diaphragm during deep expiration: *c*, liver during deep expiration; *d*, stomach during deep expiration; *e*, spleen during deep expiration. 2. Position of diaphragm during deep inspiration: *c'*, position of liver; *d'*, of stomach; *e'*, of spleen during deep inspiration; *f*, posterior vena cava as it passes through the diaphragm (Sussdorf).

has been much disputed. The external intercostals doubtless, from the direction taken by their fibres, draw the ribs forward, and by so doing increase the transverse diameter of the chest; in this respect they are regarded as inspiratory muscles. The internal intercostals, the fibres of which run in an opposite direction to the external, draw the ribs backwards and act as muscles of expiration; and speak-

ing broadly, we may say that those muscles inserted into the anterior surface of the ribs are inspiratory, whilst those inserted into the posterior edge are expiratory, from which we make the following table:

Inspiratory Muscles of the Ribs.	*Expiratory Muscles of the Ribs.*
External intercostals.	Internal intercostals.
Serratus anticus.	Transversalis costarum.
Serratus magnus (during difficult respiration).	Serratus posticus.
Levatores costarum.	

After the expiratory act there is a pause before the next inspiration. During repose the process of expiration is longer than that of inspiration, though the proportion between the two is not invariable. During work, the value of the inspiratory and expiratory acts are about equal.

During inspiration a negative pressure exists in the trachea, and during expiration a positive pressure. In the pleural cavity a negative pressure exists during expiration and inspiration, due to the attempt of the elastic lung to collapse; the value of this intra-thoracic pressure has been ascertained for the sheep to be about one-eighth of an inch of mercury, and during dyspnœa a negative pressure of three-eighths of an inch (Landois and Stirling).

We can recognise this negative pressure post-mortem by the inrush of air produced by the collapse of the lungs when the chest is opened.

The **number of respirations** will vary with the class of animal; as a rule, the larger the animal the slower the respiration:

Horse - - -	8 to 10 per minute.
Ox - - -	12 „ 15 „ „
Sheep and Goat -	12 „ 20 „ „

Rumination increases the respirations, and muscular exertion in all animals at once causes them to rise. In my own experiments on respiration this has been most marked; even walking a horse will nearly treble the number of respirations, and unless the fastest pace has been employed the

respirations fall immediately the horse stops, though they do not reach their normal for a few minutes.

The ratio of heart-beats to respiration has been placed at 1 : 4 or 1 : 5.

We have previously alluded to the influence of respiration on the circulation, and the assistance which this renders in aspirating the blood into both sides of the heart. The air drawn into the veins at the root of the neck in surgical operations is caused by this aspirating process.

Movements of Nostrils and Glottis.—Before the air reaches the lungs it is warmed by passing through the nasal cavities, so that it enters the chest at nearly the body temperature. In the majority of animals air may pass either through the nose or mouth to enter the trachea, but in the horse nasal respiration alone is possible; we therefore find in this animal the nasal chambers with their inlets and outlets well developed.

The opening into the nostrils of the horse is large and funnel-shaped, and capable of considerable dilatation; it is partly cartilaginous, and partly muscular. Immediately inside the nostril is a large sac, which does not communicate with the nasal chamber; it is termed the false nostril, and its use appears to be to simply increase the capacity of the nasal opening by allowing considerable and rapid dilatation. During forced inspiration the nostril expands, especially the outer segment, viz., that part in communication with the false nostril, and the air is rapidly drawn up through the nasal chambers. During expiration the outer segment of the nostril collapses, but the inner segment, composed principally of the cartilaginous ala, dilates. Thus one part of the nostril is principally inspiratory and one expiratory, producing a peculiar double movement of the part well seen after a gallop or in acute pneumonia.

The nasal chambers of the horse are remarkable for their great depth and extreme narrowness; the cavities are filled up by the turbinated bones, which nearly touch the septum on each side, so that a deep but extremely narrow column of air passes through the chambers, the object of which

appears to be to ensure the volume of air being raised to the proper temperature.

The air having been warmed by passing over the septum and turbinated bones enters the glottis, the arytenoid cartilages of which are separated to a greater or less extent to enlarge the opening; in quiet respiration this enlargement of the glottis is not very remarkable, but during work the cartilages are powerfully drawn upwards and backwards, and the V-shaped glottis fully opened. It is a remarkable fact that the glottal opening should be so comparatively small, considering the diameter of the trachea and the size of the nasal openings.

During inspiration the larynx and trachea slightly descend to ascend during expiration. This is particularly well seen in horses during the hurried respirations of disease, producing a well-marked rhythmical movement of the laryngeal region and base of the tongue.

Respiratory Changes in the Air and Blood.—We must now consider the changes which the air undergoes on passing into the lungs.

Atmospheric Air contains in 100 Parts:

	By Volume.	*By Weight.*
Oxygen - -	20·96	23·015
Nitrogen - -	79·01	76·985
Carbonic acid -	·03	—

The proportion of carbonic acid is small, it is a natural impurity in the air. The atmosphere also contains moisture the amount of which depends upon the temperature; the higher the temperature the greater the amount of water which the air can contain as vapour, and the lower the temperature the less the amount.

Air may be dry or saturated, the latter term implying that it contains as much vapour as it can hold at the observed temperature; it generally contains about 1 per cent. of moisture, and is spoken of as dry if it contains ¼ per cent. The air which passes from the lungs is always saturated with moisture.

When air is taken into the lungs it loses a certain proportion of its oxygen and gains a considerable amount of carbonic acid, and perhaps some other gases. More oxygen is abstracted from it than is replaced by carbonic acid, so that if both volumes be reduced to standard barometrical pressure and temperature, there is actually less air returned during expiration than entered by inspiration; owing, however, to the expansion caused by the warming it undergoes, the expired air is larger in volume than the inspired.

The proportion which the oxygen absorbed bears to the carbonic acid given off is termed the respiratory quotient, and is expressed as $\frac{CO_2}{O}$. The quotient varies with different animals, and probably depends upon the nature of the diet.

In herbivora the respiratory quotient is				·9	to 1·0
In carnivora	„	„	„	·75	„ ·8
In omnivora	„	„	„	·87	

(Munk)*

which reads thus, for every 1 part of oxygen absorbed by herbivora there is produced ·9 to 1 part of carbonic acid, and for every 1 part of oxygen absorbed by carnivora ·75 to ·8 parts of CO_2 are produced. In carnivora it will be observed that the amount of CO_2 produced is considerably less than the amount of oxygen absorbed.

We have said that there are other gases returned from the lungs besides CO_2 and O; as very little is known about these, we had better dispose of them at once. According to Reiset, both **hydrogen** and **marsh gas** are given off in the expired air of ruminants; in fact, he places the latter at 183 cubic inches in 24 hours. Both are supposed to be derived from the intestinal canal, being absorbed into the blood by the vessels of the intestinal wall. In my own experiments on the gases of respiration, I found, after deducting the oxygen, carbonic acid, and nitrogen, that a balance remained, the nature of which was unfortunately

* Quoted by M'Kendrick.

not ascertained; probably it was a mixture of these gases, and I have spoken of them as 'undetermined'; they did not, however, amount to 183 cubic inches in the 24 hours. Nitrogen in small quantities may probably be given off from the lungs of horses during rest, and Regnault and Reiset found this to be the case in dogs, though it is denied by Pflüger.

We have previously learned the changes occurring in the blood during its passage through the lungs, we have now to study the way in which the interchange of gases between this fluid and the air are brought about.

The law regulating the absorption of gases by fluids is very clear; every fluid in which a gas is soluble absorbs the same *volume* of gas, no matter what the barometric pressure may be; but as the number of molecules in a gas depends upon the pressure, it is evident that the *weight* of the absorbed gas rises and falls in proportion to the pressure. This is known as the law of Dalton and Henry.

The volume of gas absorbed by a fluid depends upon the gas; for instance, 1 volume of water will absorb 1180 volumes of ammonia gas, whilst the same volume of water will only absorb ·00193 volumes of hydrogen. The temperature of the water is also an important factor, for the higher the temperature the less the gas absorbed.

If now, instead of taking a single gas to be absorbed by a fluid, we take a mixture of gases, it is found that the volume of each gas forming the mixture is absorbed as perfectly as if it were the only gas present; no more and no less is absorbed whether the gas be by itself or whether it forms only a proportion of the mixed gases present; this is explained by Dalton as resulting from the fact that one gas does not exercise any pressure upon the other gases with which it forms a mixture, and the weight of the gas absorbed depends upon the pressure. The term used by Bunsen to define the pressure exerted by one gas in a mixture of gases is termed the 'partial pressure.' For example, 100 volumes of air contain at freezing-point and standard barometric pressure (30 inches) 21 volumes of

oxygen and 79 volumes of nitrogen: what is the partial pressure exercised by each gas in this mixture?

$$\frac{30\times21}{100} = 6{\cdot}3 \text{ inches of mercury, which is the partial pressure of the oxygen,}$$

and

$$\frac{30\times79}{100} = 23{\cdot}7 \text{ inches of mercury, which is the partial pressure of the nitrogen.}$$

The term 'partial pressure' occurs so constantly in the following pages, that the above may make the matter clearer.

If a mixture of gases, say the atmosphere, be exposed over a fluid already containing some of these gases dissolved in it, it is found that if the proportion of gases dissolved in the fluid is less than the proportion in the atmosphere above it, the latter pass into the fluid until the amount of gases in the fluid and that in the air above it are equal; but, on the other hand, if the fluid contain more dissolved gas than the atmosphere above it, gas will pass from the fluid to the atmosphere until the amounts both in the fluid and in the atmosphere are equal. This is really a process of diffusion, and it is a most important physical law in respiration, as it is the means by which the CO_2 passes from the blood into the air-cells, and the oxygen from the air-cells into the blood.

If two different gases be placed on either side of a porous partition, in a short time a complete mixture has occurred, as both gases will pass through the porous diaphragm in opposite directions until a complete and equal mixture has occurred. This is termed the process of diffusion, and is the chief means by which the air in the deeper part of the lungs mixes with the fresh air introduced by breathing.

Such are the physical laws which it is necessary to understand before the processes involved in respiration can be fully comprehended.

The blood having been robbed of oxygen in the tissues, the hæmoglobin makes its way back to the lungs in a partly

reduced condition; here it circulates through the vast capillary system spread over the alveoli of these organs, and is brought as closely as possible into contact with the air in the ultimate air-passages. Between it and the air we have only the membrane of the air-sac and the wall of the capillary, both of which are bathed in fluid; through this wet membrane the oxygen instantaneously passes, being greedily absorbed by the hæmoglobin of the red cells; the gas must, of necessity, first pass into the blood plasma, and from here it is taken up by the red corpuscles.

The oxygen is not simply absorbed by the red cells but forms with the hæmoglobin a weak chemical compound, for experiment has clearly shown that the union of hæmoglobin with oxygen is largely independent of pressure, and therefore does not obey the law of Dalton and Henry, which it certainly would do if simply absorbed.

We have yet to learn why it is that the oxygen in the air vesicles rushes into the capillaries to form this chemical union with hæmoglobin. Here we have one of the physical laws brought into play which we have previously described. When the venous blood arrives in the lungs it has lost much of its oxygen, the partial pressure of the oxygen is low, whereas the partial pressure of the oxygen in the atmosphere of the air-cells is high; the result of this is that practically instantaneous diffusion occurs through the moist membrane separating the gas and the fluid. The oxygen entering the blood plasma unites at once with hæmoglobin, this latter taking up all or nearly all the oxygen it is capable of holding, (an amount which is infinitely greater than if simple absorption of oxygen by hæmoglobin occurred), and distributes it to the tissues through the medium of the arterial circulation.

The tissues are greedy for oxygen, their oxygen pressure is practically *nil*, once more the physical law of diffusion occurs; the high partial pressure of the oxygen in the arterial blood becomes, through loss of oxygen in the tissues, low partial pressure in venous blood, and the partly reduced hæmoglobin rushes to the lungs, when the

process just described is repeated. But the loss of oxygen in the tissues is not the only change the blood undergoes, for not only is its hæmoglobin reduced, but as the outcome of tissue activity increased quantities of another gas are added to it, the gas alluded to is carbonic acid; this is largely taken up by the venous blood and conveyed to the lungs, and the method by which it is got rid of will be presently explained.

The changes occurring to the oxygen in the tissues are quite unknown; it is supposed to be stored up in some way or other until required. It has been suggested that the storing up in the tissues may be closely allied to the storing up of oxygen by hæmoglobin, though with this difference, that the tissue oxygen-holding substance is more stable than the blood oxygen-holding substance. All we do know of the fate of the oxygen is that it eventually assists in producing certain changes in the tissues, which lead to the production of carbonic acid and other substances; but the changes which the oxygen undergoes from the time, to use the words of Professor Foster, it slips from the blood into the muscular substance, to the moment it issues from the tissues united with carbon as carbonic acid, constitute the whole mystery of life. We do know, however, that the oxidations take place in the tissues, and not in the blood as was formerly supposed.

In the systemic capillaries the partial pressure of the carbonic acid is lower than the partial pressure of this gas in the tissues, the result of which is that it is hurried into the blood by the process of diffusion; but here, as with oxygen, simple absorption of the gas by the plasma would not be sufficient for the purpose of carrying off the whole of the CO_2 resulting from tissue activity. Now, although there is no compound of CO_2 and hæmoglobin definitely known, still there is a substance in the blood capable of fixing CO_2 until the lungs are reached.

If the serum of blood be exposed to the vacuum of an air-pump, it is found to yield little oxygen but a quantity of CO_2; it yields but little O, because, as we have already

learned, this is combined in the red cells, but the fact of its yielding large quantities of CO_2 points to the blood plasma as the chief means by which this substance is carried.

It has been determined experimentally that blood plasma will absorb more CO_2 than the same quantity of water, and it is evident, therefore, that there is something in the plasma which assists in carrying the CO_2; this something has been variously stated, but it is generally believed that the sodium carbonate of the blood unites with a portion of the carbonic acid, though other substances may assist. Between the amount absorbed in the plasma, and that held in chemical combination by certain salts of the plasma, the total amount is carried along in the venous blood stream, the partial pressure of the CO_2 in the fluid being high; on arriving at the lungs it circulates through the capillary network spread over the walls of the alveoli, the same wet membrane existing between it and the external air as was described in speaking of the oxygen.

The partial pressure of the CO_2 in the air of the air-sacs being much lower than that of the blood, diffusion occurs between the blood and the air, the CO_2 passing out until equilibrium is established. The air now in the alveoli of the lungs having lost some of its oxygen, and considerably gained in its carbonic acid—in other words, having the partial pressure of its gases altered—diffusion between the air in the ultimate air-cells and bronchial tubes rapidly occurs until the balance is restored, and the air in the alveoli rendered fit for further blood-reviving processes.

Before closing this part of the subject it is necessary to allude to the manner in which the combined oxygen is liberated in the tissues, and the combined CO_2 liberated in the lungs, so that the law of diffusion may act, this being, as we have now learned, the chief process by which the balance of gases in these regions is restored.

Certain gases have a tendency to leave the substances with which they are united when the pressure upon them becomes reduced, this process is termed 'dissociation'; it

liberates the oxygen in the tissues, and assists in liberating the CO_2 in the lungs from the substances with which these are chemically combined, viz., hæmoglobin and carbonate of soda.

When an animal is compelled to breathe the same air over and over again, there is a gradual loss of oxygen and increase in carbonic acid, and though death will ultimately ensue unless the air be renewed, it is remarkable that before this occurs nearly the whole of the oxygen will have been consumed from the atmosphere, which is further evidence, if any be needed, that the oxygen is not simply absorbed by the blood, and that it does not obey the laws of pressure. Experimental inquiry has proved that animals may live in an atmosphere containing only 14·8 per cent. of oxygen, but that rapid asphyxia follows when the oxygen falls to 3 per cent.

By increasing the amount of oxygen in a mixture over and above that contained normally in air, the blood cannot be made to take up much more oxygen than if the normal amount only were present; a pressure of ten atmospheres only causes an increase of 3·4 per cent. absorbed, so that the blood contains 23·4 per cent. of oxygen instead of 20 per cent. The practical application of this fact in the treatment of certain diseases by the inhalation of oxygen is obvious: if we double the amount of oxygen in the air, less than 1 per cent. of the extra addition is absorbed.

Apnœa may be produced by distending the lungs several times with air, and holding the breath; during this period the respiratory centre is controlled by certain impulses occurring through the vagus.

Dyspnœa is increased respiration due to an insufficient quantity of oxygen in the blood.

If the air supply be entirely cut off, asphyxia and death rapidly ensue. **Asphyxia** has been divided into three stages. In the first stage the attempts at breathing are laboured and painful, deep and frequent, and all the respiratory muscles, including the complemental ones, are brought into play; convulsions occur, and the blood pressure rises. In the

second stage the inspiratory muscles are less active, the expiratory still powerful, and the convulsions cease. In the third stage the animal lies unconscious, occasionally gasping, the mouth open (even in the horse), the pupils dilated, the pulse barely perceptible or absent. During this stage the blood pressure rapidly falls. Death occurs in from five to six minutes from the commencement of the first stage.

The **Nervous Mechanism** governing respiration may temporarily be under the control of the will, but under ordinary circumstances is independent of it. The respiratory centre lies in the medulla, close to the deep origin of the pneumogastric nerves; it is supposed to consist of an inspiratory and expiratory portion, and there are good reasons for believing that the pneumogastric contains fibres which lead to expiratory efforts on the one hand, and inspiratory on the other. From experimental inquiry, it is certain that the vagus contains fibres which may have the effect of controlling and augmenting respiration. But the nervous mechanism is by no means so simple as the above statement might suggest. The number of muscles brought into play during the respiratory process, and the exact order in which they must work, necessitate the most careful co-ordinating nervous arrangement, and that will be fully brought home to us when we consider that the respiratory wave from the nostrils to the diaphragm, and from the abdominal muscles to the nostrils, must be evenly and regularly performed.

Further, the nervous influences concerned in the process are complicated by their connection with the spinal cord, which under some conditions has been known to carry on the respiratory process independent of the centre in the medulla, though under ordinary circumstances destruction of the centre in the medulla means instantaneous death.

If the spinal cord be divided below the origin of the phrenic nerves there is paralysis of the intercostal and abdominal muscles, but the action of the diaphragm is rendered stronger, while expiration is carried out by the

elastic recoil of the chest wall and lungs; division of one phrenic nerve leads to paralysis of one half of the diaphragm, and of both nerves to complete cessation of its action, inspiration being carried on by the muscles which elevate the ribs. Division of both vagi in the neck leads to a modification of the respiratory process though it still continues, and division of the cord below the medulla does not interfere with the facial and laryngeal movements.

Sussdorf states that division of the phrenic nerves in the horse leads to increased respiration, difficulty in breathing, the latter being chiefly thoracic; increased heart's action, and the fæces collect in the rectum. In about 24 hours these symptoms pass away, and if the animals be worked no appreciable difficulty in breathing is observed. The result of the operation is fatty degeneration of the muscular portion of the diaphragm.

The respiratory centre is considerably affected, not only by the nervous influences conveyed to it, but by the quality of the blood circulating through it. The violent respiratory efforts observed in the second stage of asphyxia are said to be due to the deoxidized condition of the blood circulating through the medulla. At one time it was supposed that the excess of carbonic acid in the blood stimulated the expiratory centre, whilst a deficiency of oxygen stimulated the inspiratory movement; this view is not generally held at the present day, or only partly believed to be true. The changes in the blood no doubt lead to stimulation of the respiratory centre, but whether these changes are due to the difference in the composition of the blood gas, or to some other substance circulating in the fluid, is not known. It has been suggested that sarcolactic acid, which is produced as the result of muscle activity, may increase the respiratory movements and explain the increased respiratory activity which, as we know, accompanies rapid work.

The Quantity of Air breathed.—The amount of air passing into a horse's lungs in an hour during perfect repose amounts to about 80 cubic feet; it is sometimes much

higher than this; the largest amount I ever obtained was 145 cubic feet per hour. Assuming that the animal breathes ten times per minute, the amount of each inspiration may be taken at 230 cubic inches. It is to be noted that the amount of air expired, even under apparently identical conditions, is liable to great variation. We have no means of knowing the amount of the residual, reserve, or complemental air which may be used.

Respiratory experiments have been made on nearly all animals. I will principally confine my remarks to the horse, on which some very extended observations have been carried out.

100 *parts of inspired air contain:*

Oxygen	20·96
Carbonic acid	·03
Nitrogen	79·01

100 *parts of air collected from the lungs during repose contain:*

Oxygen	18·96
Carbonic acid	1·25
Nitrogen	79·01
Undetermined gases	·78

The expired air has thus lost 2 per cent. of its oxygen, and has gained 1·22 per cent. of CO_2. In other words, it leaves the lungs containing about forty times more CO_2 than when it entered, in addition to which there is added $\frac{3}{4}$ cubic foot of gases of unknown composition—probably a mixture of nitrogen, hydrogen, and marsh gas.

More oxygen is absorbed than CO_2 expired, and my observations show that the respiratory quotient for the horse at rest is ·69, a figure which is much lower than that generally quoted, viz., ·9 (see p. 84).

If we take the CO_2 of repose at $1\frac{1}{4}$ cubic feet per hour for a horse, the carbon of this would be equal to 293 grains, or $14\frac{3}{4}$ ozs. in 24 hours.

These results, however, do not agree with those obtained by Zuntz and Lehmann in Germany.* The horses used by

* Ellenberger's 'Physiologie.'

these observers absorbed more oxygen and gave out more carbonic acid than the English cavalry horses with which I worked, and according to their experiments the amount of carbon produced by a horse in 24 hours is about 25½ ozs. Here is a table of my own, showing the respiratory changes for one hour in a horse during perfect repose:

Cubic feet of air per hour	74·25
Carbonic acid expired per hour in cubic feet	1·63
Oxygen absorbed per hour in cubic feet	1·13
Undetermined gases	·429
Respiratory quotient	·69

There are certain conditions which influence the production of carbonic acid, of which the most important is muscular work. As the result of increased muscular activity the production of carbonic acid is considerably increased. This increase is carried away by the blood-stream, and got rid of at the lungs as previously explained. It is evident that the more severe the work, or the greater the strain thrown on the muscles, the greater the amount of CO_2 produced. I have endeavoured to ascertain what this amount is for each pace of the horse, and the results of a large number of observations are embodied in the following table:

	Air expired per hour in cubic feet.	CO_2 *expired per hour in cubic feet.*	O *absorbed per hour in cubic feet.*	*Respiratory Quotient.*	*Undetermined Gases in cubic feet per hour.*
Walk	133·55	1·08	2·04	·5327	·7568
Trot	987 87	3·98	6·47	·5917	2·5060
Canter	390·1	4·9	8·35	·5959	3·3087
Gallop	849·1	14·97	26 07	·5743	6·6955

The above table does not agree with the elaborate researches of Zuntz and Lehmann, but, then, the work performed by their horses was executed on a revolving platform, whereas work of a normal kind was performed by the

animals experimented upon by me, though of necessity some slight loss must have occurred in the short time elapsing between the termination of the work and the communication made between the animal and the respiratory apparatus.

I was surprised to find how greatly the respiratory products at the same pace and in the same horses varied, and I do not believe it to be possible to obtain anything like exact results with animals performing work in a natural manner.

M'Kendrick, quoting from Munk, gives the following table of respiratory changes in animals :

Gases of Respiration in 24 Hours.

	Body Weight.	*Oxygen in cubic feet.*	*Carbonic Acid in cubic feet.*
Ox -	1,322 lbs.	196	196
Horse -	991 „	150	171
Sheep -	154 „	20	20

The oxygen requirements of an animal bear no proportion to its size : a small singing-bird will use up, per unit of body weight, ten times as much oxygen as a hen. In the human subject it has been shown that the nature of the diet influences considerably the amount of CO_2 excreted and O absorbed. The CO_2 is increased by giving food rich in starch ; fats have not such a marked effect in this direction, whilst albuminoids increase the absorption of oxygen.

CHAPTER VII.

DIGESTION.

Prehension of Food.—The horse carries the food into the mouth by means of his lips, which are highly endowed with nerves and extremely muscular, the upper being the stronger of the two. When grazing, the fodder is first bitten off by means of the incisor teeth, and then carried into the mouth by the lips. The upper lip of the horse being solid he cannot bite close to the ground, and it is a matter of common remark that he starves where sheep thrive.

The extreme delicacy of touch with which the lips are endowed serves a highly beneficial purpose; the long hairs growing from the muzzle are all in contact with nerve-endings in the skin.

In the choice or rejection of food the horse is mainly guided by the sense of smell. When grazing, the animal invariably extends and flexes one fore-leg to enable it to reach the ground, which, owing either to the shortness of neck or the length of leg, it is unable to reach otherwise.

In the ox the tongue is the organ of prehension; it is protruded and passed round the blades of grass, which are nipped off between the incisor teeth and the dental pad.

The food having been carried into the mouth, is passed between the teeth by means of the tongue. A considerable anatomical difference exists between the tongue of the horse and that of the ox, the most remarkable, perhaps, being the smoothness of the one and the extreme roughness of the

other. The papillæ of the tongue will be dealt with in speaking of Taste.

The prehension of liquids is caused by the formation of a vacuum in the mouth by the pumping action of the tongue, whilst the lips are kept tightly sealed, excepting an opening left in the front which is kept below the level of the water. At each swallow the ears are drawn forwards, and during the interval they fall backwards.

During **Mastication** certain movements of the jaws are performed, to admit of which the articulation of the upper and lower jaw is exceedingly large. The disc of cartilage placed here between the two bones is to save the parts from injury, and to admit of the extensive lateral or rotatory motion so marked in the herbivora.

It is singular to observe that the upper jaw in the horse is so much wider than the lower one; the upper molar teeth are also much larger. Owing to this, the tables of the teeth instead of wearing with a level surface, present a very oblique and chisel-shaped arrangement, the upper teeth being sharp on the outside, the lower row of teeth on the inside. This is an important clinical fact, sharp teeth giving rise to much trouble and suffering.

Mastication in both horse and ox is lateral and somewhat rotatory; that is to say, after the teeth have crossed each other from left to right, or *vice versâ*, the mouth is opened, and the molars brought back to their original position. In the horse the lateral movement occurs from left to right, or from right to left, never from rear to front, or front to rear. Mastication occurs on one side only, and when that gets tired the food is passed to the other. One side takes a long time to tire; mastication may be performed for a whole hour in one direction.

In the peculiar lateral movement of the jaws of the horse and ox, the changes which occur in the articulation have been pointed out by Gamgee* to be as follows: During the rotatory movement, or lateral displacement, one of the

* 'Our Domestic Animals in Health and Disease.'

articulating heads remains as a fixed point, simply turning on its centre, whilst its fellow describes an arc. This is why the movement can only occur on one side at a time. The same observer, noticing the one-sided mastication in the ox, states that the first stroke of the molars is in an opposite direction to the regular action which follows. Thus, if masticating from right to left the first stroke is made from left to right.

My own observations on the movements of the articulation of the horse do not agree with Gamgee's. On opening the mouth preparatory to masticating (say from right to left), the right articulation at once rises, the left becomes depressed, and the contents of the orbital fossa on this side bulge; the teeth now crush from right to left, the right articulation descending, the left ascending. As the right teeth meet the right orbital fossa ascends; by standing in front of the horse we can observe that the elevation of the fossæ is alternately performed, that one on the side opposite to the masticating surface bulging the most.

In the horse mastication is slow, and as a rule well performed; it takes a horse from five to ten minutes to eat one pound of corn, and fifteen to twenty minutes to eat one pound of hay. In the ox the food does not undergo the same amount of preliminary crushing, as by the process of rumination it is brought back to the mouth for remastication.

The muscles which close the mouth are the masseter internus and externus, temporalis and pterygoideus; those which open it are the sterno- and stylo-maxillaris and digastricus.

The extensive development of the molar teeth in all herbivora can be readily understood, when we remember the wear and tear to which they are exposed in crushing the fibrous portion of plants.

The molars wear away more rapidly than the incisors, due to the fact that they perform more work. They become so much reduced in length that they would not meet were it not that the incisors become more oblique.

It is a remakable fact that in all herbivora the teeth never leave off growing; if one molar be removed its fellow in the lower jaw, through the absence of friction, grows into the space left. This is a practical fact of clinical importance. In the incisor teeth the changes due to constant growth assist in determining the age.

Deglutition comprises three stages. In the first stage the food is passed backwards by means of the tongue under the soft palate, which is raised to allow it to pass; in the second stage, the tongue is drawn upwards and backwards, the pharynx and larynx are advanced, and the base of the tongue and bolus close the epiglottis. The soft palate, which in the horse reaches well into the pharynx, is still up and cuts off the communication with the nose; without this provision both food and water would return by the nostrils. In the third stage, the bolus is grasped by the pharyngeal muscles, which contract on it from before backwards and gradually pass it along the œsophagus, either with or against gravity. In the horse and ox the passage of the bolus along the channel of the neck can be distinctly seen.

Part of the act is under the control of the will, but once the food reaches the fauces the action is entirely reflex; the closure of the glottal opening and the presence of food in the pharynx excites the action of swallowing, which is a purely reflex condition the centre for which exists in the medulla. The pharyngeal muscles are remarkably strong and stoutly grip the bolus.

Though the epiglottis closes the glottal opening, this closure is not absolutely essential to swallowing. When the epiglottis has been removed the base of the tongue takes its place; but horses can swallow when the glottis is open —for example, when the arytenoid cartilage has been removed.

Owing to the length of the soft palate in the horse, food rejected from the stomach or unable to pass along the œsophagus can only be returned by the nostrils.

Though the passage of food along the œsophagus is com-

paratively a slow process, the passage of liquid, on the other hand, is very rapid. As many as sixty movements may be made in a minute, the motion being capable of occurring against gravity—for example, when an animal drinks from the ground.

The process of swallowing solids is facilitated by the saliva. Thus, when the salivary secretion has been experimentally diverted, swallowing only occurs with difficulty and very slowly.

The upper portion of the œsophagus for two-thirds of its length is composed of striped muscular fibre, though not under the control of the will; the lower or posterior third consists of unstriped muscle and is exceedingly thick.

The nervous mechanism employed in swallowing is very complicated. The swallowing centre, which is situated in the medulla and pons Varolii, has to be stimulated, and the muscles employed have to act regularly and in their proper order.

The reflex act of swallowing is as follows: By means of the sensory glosso-pharyngeal and superior laryngeal nerves an impression is conveyed to the brain of the presence of material in the pharynx; a motor impression is then sent out, putting in action the motor fibres of the glosso-pharyngeal supplying the muscles of the pharynx, and causing them to contract.

The tongue is supplied with sensation by the glosso-pharyngeal, and portions of the fifth pair; the pharynx by the glosso-pharyngeal, and the opening into the larynx by the superior laryngeal. The motor nerves of the tongue are the hypo-glossal, inferior maxillary division of the fifth and branches of the facial. The palate is supplied by the pharyngeal plexus formed by the vagus, glosso-pharyngeal, and sympathetic; the glosso-pharyngeal supplies the muscles of the pharynx with motor powers, and the branches of the fifth supply the muscles of mastication.

In ruminants swallowing is carried on by the same physiological process. Both the mouth and pharynx are very large and wide, and the œsophagus of considerable

diameter; the food can therefore be swallowed not only with rapidity but with ease, which the physiological condition of the stomachs of these animals requires. Reversed muscular action of the œsophagus assists the process of rumination.

The Saliva.

During the process of mastication the food becomes mixed in the mouth with a fluid known as the saliva; the secretion of which occurs in three distinct pairs of glands. The method by which it is formed is important for us to understand, as much the same process occurs in other secretory glands which we have not the same opportunity of watching during activity.

The three glands which secrete saliva are the parotid, submaxillary, and sublingual; and these are divided into two systems, anterior and posterior. The former comprises the submaxillary and sublingual; the latter the parotid. The two systems are further divided into mucous and serous (or albuminous), the submaxillary and sublingual being types of the first, the parotid the type of the last.

The salivary glands in the herbivora are of considerable size, the anterior system in the ox being well developed, whilst in the horse it is rudimentary. According to Colin, there is no connection between the weight of the glands and the amount of fluid they secrete. The parotid in all cases secretes more than the others; in the horse it is four times heavier than the submaxillary, but it secretes twenty-four times as much saliva. In the ox the parotid is not so large as the submaxillary, but it secretes four or five times as much saliva. The same observer places the daily secretion of saliva in the horse at 84 lbs., and in the ox at 112 lbs., though the amount will vary depending on the nature of the food consumed; thus, hay absorbs more than four times its weight of saliva, oats rather more than its own weight, green fodder half its own weight. The amount of saliva secreted, therefore, depends on the dryness of the food.

Mixed saliva is an opalescent or slightly-turbid fluid which readily froths. On standing it throws down a

deposit of carbonate of lime due to the removal of its carbonic acid; in reaction it is alkaline, and its specific gravity is 1005 in the horse, and 1010 in the ox. Saliva examined microscopically is found to consist of granules, epithelial cells, bacteria, and salivary corpuscles.

About ·6 per cent. of the saliva consists of mineral matter, and ·2 per cent., more or less, of organic matter; the latter consisting of mucin, which gives saliva its well-known viscidity and ropiness, and proteid bodies of the serum albumin and globulin class. We make no mention of ptyalin, a substance of which we shall shortly speak, as it is doubtful if it exists in the herbivora, and under any circumstances its amount has not been determined.

Lassaigne gives the following analysis of the mixed saliva of the horse and ox:

	Horse.	*Ox.*
Water - - -	992·00	990·74
Mucin and albumin - -	2·00	·44
Alkaline carbonates - -	1·08	3·38
„ chlorides - - -	4·92	2·85
„ phosphates and phosphate of lime (traces) -	—	2·59

Lehmann gives the following analysis of horse saliva from the parotid:

Water - - - - -	990·00
Solids - - - - -	10·00
Mucin and epithelium / Soluble organic matter) - -	4·00
Salts - - - -	6·70

The salts of saliva are principally carbonate of lime, alkaline chlorides, and phosphate of lime and magnesia. A substance known as sulphocyanide of potassium has been found in minute quantities in the saliva of the human subject, but is absent from that of the horse.

The gases of the saliva are principally carbonic acid with traces of oxygen and nitrogen. There is no fluid in the body which contains so much CO_2 as saliva.

The three salivas secreted have different physical properties. Parotid saliva is watery, clear, free from mucin, but containing a small quantity of proteid. Submaxillary saliva is clear, viscid, contains formed elements, and in those animals the saliva of which is amylolytic it possesses ptyalin. The sublingual is more viscid than the submaxillary, and contains more formed elements and organic salts.

Colin has observed certain peculiarities in the salivary secretion of herbivora which deserve our careful attention. He has discovered that the secretion from the parotids is unilateral; the gland on that side of the mouth on which the horse is masticating secretes much more than on the opposite side; the parotid on the masticating side gives two or three times as much as its fellow; the submaxillary and sublingual glands, on the other hand, secrete equally, no matter on which side mastication is being performed. Further, the parotids secrete during rumination, the unilateral secretion still being maintained, whilst the submaxillary and sublingual glands are during this process in a state of rest. In a fasting horse the parotids are quiet, whilst in the ox they are active; and observations tend to show that in both animals during fasting the mouth is kept moist by secretions from the sublingual, palatine, and molar glands. These latter glands of the mouth are extensively developed in the horse, particularly the palatine and some large glands close to the epiglottis; their secretion is viscid.

Neither the sight of food nor the introduction into the mouth of sapid substances produce any effect over the salivary secretion from the parotid of the horse. Sapid substances, however, stimulate submaxillary secretion.

The use of the saliva in the herbivora is essentially that of allowing of perfect mastication and lubrication of the anterior digestive tract, of stimulating the nerves of taste, and in ruminants assisting in rumination; according to my observations on the horse it has no chemical action on the starch of food. So intimately, however, is salivary secretion associated with starch conversion, that it is not possible to pass over without further notice the action produced on

starch in man and the dog, and according to some observers in horses and cattle, by the presence of ptyalin in the saliva.

If boiled starch be mixed with filtered human saliva and kept at a temperature of 95° F., in a short time the characteristic reaction of a blue colour with iodine disappears, and a reddish colour is formed on the addition of this reagent, indicating the presence of a substance known as erythrodextrin. At this time the fluid, which before was sugar-free, now contains distinct evidence of its presence; by continuing the action of the saliva it is found that shortly the red colour on the addition of iodine has disappeared, and the fluid now contains a considerable proportion of sugar. Analysis shows that for the amount of starch employed the full amount of sugar has not been obtained; in other words, there is a second substance present in addition to sugar as the result of the action of the saliva, and this is described as achroodextrin. The sugar formed from starch by the action of saliva is not grape-sugar but maltose, glucose (dextrose or grape-sugar) only being found in small quantities if at all.

This action of the saliva on starch is described as the **Amylolytic** action; it is due to the presence of **Ptyalin** which acts the part of a ferment. The process is destroyed by a high or low temperature, retarded by a slightly acid or alkaline medium, and destroyed by free hydrochloric acid.

If starch be boiled with a dilute acid conversion into sugar occurs; but the difference between the action of this and saliva is, that whereas the latter can only produce maltose the acid produces dextrose.

The view I hold as to the non-amylolytic action of saliva in herbivora is not supported by other observers. Ellenberger* distinctly states that both the parotid and submaxillary saliva of the horse and ox can convert starch into sugar, but in the case of the horse it is only the saliva first secreted by the gland after a rest, which possesses this property to a high degree; as secretion proceeds the power

* 'Physiologie der Haussängethiere.'

is nearly, though not entirely, lost. Ellenberger's observations are so reliable that we are bound to accept as a fact that at some period of digestion horse saliva may possess amylolytic properties.

Meade Smith* states that the saliva of the horse will convert crushed raw starch into sugar in fifteen minutes, and that the process will continue in the stomach (where the early acidity, according to Ellenberger, is due to lactic and not hydrochloric acid); he further states that horse saliva will convert cane into grape-sugar. In ruminants he believes the starch conversion takes place both in the mouth and rumen.

Though I do not accept these views, we shall shortly show how starch is converted into sugar in the horse's stomach.

Secretion of Saliva.—The mechanism concerned in the secretion of saliva deserves our careful attention, for the reason that it throws considerable light on other secretory processes. It has been worked out by so many competent observers that the leading points in its action are beyond all doubt. The submaxillary gland of the dog has afforded the desired information, and we have reason to believe that the same process holds good for the parotid and other glands, both of this animal and herbivora.

The chief point in the secretion is that it is controlled by the nervous system, and is independent of the blood pressure in the gland. Afferent nerves, viz, the gustatory division of the fifth and the glosso-pharyngeal, convey from the mouth to the medulla a certain sensation, which by means of an efferent nerve is conveyed to the gland and secretion results. The efferent nerve of the submaxillary gland of the dog is supplied by the **chorda tympani**, a small branch given off by the seventh cranial nerve which enters the gland at its hilus, and supplies the vessels with dilator and the cells with secretory fibres. How the nerve terminates in the gland is unknown. The second nerve supply-

* 'A Text-book of Comparative Physiology.'

ing the submaxillary gland is a branch of the sympathetic, which spreads out and invests with constrictor fibres the walls of the artery supplying the part.

Thus the chorda tympani supplies the gland with secretory fibres, and the walls of the vessels with dilator fibres, whilst the sympathetic supplies the vessels with constrictor fibres, and only a few secretory fibres.

If the chorda be stimulated the vessels dilate, the gland becomes red, the blood flowing from the veins is arterial in tint, and the veins pulsate. In addition to this, there is an abundant secretion of watery saliva poor in solids. When the sympathetic is stimulated the vessels contract, only a small quantity of extremely viscid saliva flows which is rich in solids, the blood in the veins becomes very dark in colour, and the blood-stream slows.

That the increased flow of blood to the gland produced by irritating the chorda does not produce the secretion, is proved by the fact that the pressure of the saliva in the duct of the gland is higher than the blood pressure outside the gland. Further, if before stimulating the chorda some atropine be injected, stimulation of the nerve still produces to the full all the vascular changes, but not a trace of saliva is secreted. Hence, secretion is not due merely to increased blood pressure.

This atropine experiment proves the existence in the chorda of the two sets of nerves, viz., of the secretory and the vaso-dilator. Through the atropine the secretory are paralysed, the dilators are not. Atropine does not affect the action of the sympathetic nerve.

Twenty-four hours after the chorda has been divided a watery secretion occurs, not only on the side operated upon but on the opposite side also; this has been termed paralytic secretion, it diminishes about the eighth day.

Though the action of the nerves on the submaxillary gland is universally accepted, great difference of opinion exists as to how they act. Heidenhain's view is that a gland is supplied with a trophic nerve which excites chemical changes in the protoplasm, and a secretory nerve which

separates the manufactured products. Building up, anabolism, and breaking down, katabolism, are occurring constantly in all the cells of the body. The cranial nerves are chiefly secretory, whilst the sympathetic are trophic, hence stimulation of the chorda gives a watery saliva poor in solids, whilst stimulation of the sympathetic gives a scanty saliva rich in solids.

Langley considers that this view is not tenable, and that it is more reasonable to believe that there is only one kind of fibre engaged in secretion, which, being mixed with nerves having opposite actions on the bloodvessels, produces the difference in the results observed.

During secretion the temperature of the gland rises 2·7 F., and the blood in the veins is warmer than the blood in the arteries.

The method by which secretion in the parotid gland is carried out differs in no essential respect from that of the submaxillary. The nerves supplying the parotid are the glosso-pharyngeal (the action of which corresponds to the chorda of the submaxillary) and the sympathetic; both of these contain secretory fibres and dilator and constrictor nerves for the bloodvessels.

The **changes occurring in the cells** of the salivary glands during secretion depend upon the nature of the gland. We will therefore describe separately, from Langley's observations, the changes in the cells of a serous gland, such as the parotid, and the changes in a mucous gland, of which the submaxillary is a type. In both we distinguish certain differences depending upon whether the gland is at rest or whether it is active, viz., whether the cells are charged or whether they are rapidly getting rid of the material which has been formed. In connection with this point, we must remember that differences in the cells may be observed which are more accidental than real, and depend upon the methods which have been employed in demonstrating them. Discordant results are not, however, obtained when by suitable means the gland-cells in the living animal are examined during rest and activity.

During the stage of rest in a living serous gland, the cells are found to be filled with a quantity of granular material, and the outline of each individual cell is indistinct; the lumen of the gland is also occluded, and no nucleus can be observed in the cells; in other words, the gland is charged

Fig. 5.—Changes in the Cells of the Living Parotid during Secretion.

A, at rest; B, in the first stage of secretion; C, after prolonged secretion (Foster, after Langley).

with its secretory products (Fig. 5, A). During activity the cells get rid of their granular material, which gradually passes towards the centre of the acinus or lumen, leaving each cell with a clear outer edge, whilst that edge next the lumen is still granular (Fig. 5, B). In an exhausted

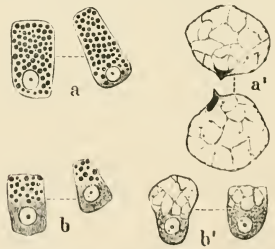


Fig. 6.—Cells from Mucous Gland.

a, from loaded gland; b, from discharged gland; a', b', treated with dilute acid; a', from loaded; b', from discharged gland.

condition the cells are remarkably clear, only a few granules being left in them on that edge next the lumen, which latter is now distinct and large, and the nuclei are clearly seen occupying a central position (Fig. 5, C).

If a mucous gland at rest be examined under like condi-

tions, the cells are found filled with granules much larger than those of a serous gland, and a nucleus is seen occupying one edge of the cell (Fig. 6, a). During activity the granules are passed into the lumen of the gland, but they do not leave behind them in the cells the same clear space seen in the serous cell (Fig. 6, b). If the cells while in an active condition be acted upon by water or dilute acetic acid, they swell up and become transparent owing to the mucin they contain, and a delicate network is seen to invade the cell (Fig. 6, a'). A similar appearance is produced in the exhausted cell (Fig. 6, b'), excepting that less transparent mucin is seen and more granular substance, whilst the nucleus of the exhausted irrigated gland is seen passing towards the centre of the cell instead of remaining towards the outer wall.

In hardened specimens of mucous glands, towards the outer edge in some of the acini, cells may be found shaped like half-moons or crescents, but are not loaded with mucin, since they stain with carmine which stains mucin with difficulty. These crescents of Gianuzzi are not found in hardened preparations of serous glands.

The outcome of these changes proves that the organic elements found in the salivary secretion are manufactured by the cells in the glands, whilst the inorganic constituents are probably the result of the transudation through the cells, of the lymph which reaches them through the lymph passages, though experiments made by Langley and Fletcher* go to prove that even water and salts are the result of an act of cell secretion and not of mere transudation.

Stomach Digestion.

The subject of stomach digestion in the horse has been worked out only by means of feeding experiments, as it has been found impossible to establish a gastric fistula in this animal owing to the distance the stomach lies from the abdominal wall; pure gastric juice has, therefore, probably never been obtained from the horse.

* Phil. Trans., 1889, vol. clxxx., B., p. 109. Quoted by Halliburton.

It is to Colin, Ellenberger, and Hofmeister that we owe nearly all we know about the physical and chemical changes occurring in the stomach, these observers having experimented with different foods on a large number of animals which were destroyed at certain intervals. Working on the same lines, I have for many years carried on, as opportunity occurred, observations of a similar nature. In this way a large number of facts have been obtained, a summary of which can only be embodied in this chapter.

The first peculiarity to be noticed in soliped digestion is that the stomach is rarely empty; no matter at what period of digestion observations are made, food is still to be found in it. It is only when horses have purposely been deprived of nutriment for not less than twenty-four hours that an empty stomach can be obtained. On the other hand, feeding experiments show that very shortly after food arrives in the stomach it commences to pass out, and the difficulty thus presented to the observer in reconciling these opposite facts is at first sight insuperable.

It is perfectly true that food does pass out early, it is equally true that it is long retained; these opposite conditions are the result of the periods of digestion. When food enters an empty stomach it passes towards the pylorus, where it meets with a fluid of an alkaline or neutral reaction which has come from the mouth. As more food is consumed some commences to pass out at the pylorus into the bowel, the amount passing out not equalling at present the amount passing in; the stomach becomes gradually distended, and when two-thirds full, which is the condition in which the most active digestion occurs, the amount passing out will, if more food be taken, equal the amount being swallowed, so that we have a stream of partially peptonized chyme streaming out of the right extremity, while a corresponding bulk of ingesta is entering the inert left sac. In fact, the stomach may pass out during feeding two or three times the bulk of food remaining in it when the feed is finished. Let us suppose now that by this time the 'feed' is finished; at once the passage of chyme into the

duodenum ceases, or becomes so slowed down that only small quantities of material pass out, and so slowly will this occur that it will be many hours before the stomach is really empty, though had the process continued as it commenced, it would not have contained anything at the end of an hour.

This condition of stomach digestion in the horse may be variously modified depending on the nature of the food, the quantity given, the form in which it is given, the order in which one food follows another, and whether water be

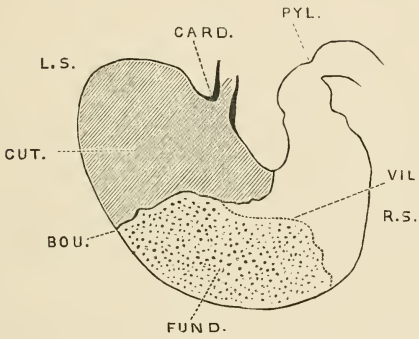


FIG. 7.—LONGITUDINAL SECTION OF THE STOMACH OF THE HORSE. CARD., cardia ; PYL., pylorus ; L.S., left sac ; R.S., right sac ; CUT., cuticular coat ; VIL., villous coat ; BOU., boundary line between the cuticular and villous portions ; FUND., fundus of the stomach : the dotted area indicates the position of the secretion of gastric juice.

given before or after feeding. All these are points which require our attention, but before giving it we must briefly look at the stomach itself.

The mean capacity of a horse's stomach is, according to Colin, from 25 to 30 pints, or from ·5 to ·63 of a cubic foot. These figures are obtained from a very large number of observations, and give the extreme size of the organ when distended. The viscus is under the best conditions for

digestion when it contains about 17½ pints, or is distended to two-thirds of its capacity.

The mucous membrane of the stomach of the horse is peculiar; one portion of it, practically half, is a continuation of the membrane of the œsophagus; this ends abruptly, and then the villous coat commences which runs to the pylorus. It is in this coat that a true digestive juice is secreted though not from the entire surface, for on examining the villous membrane it is found to differ greatly in appearance, the fundus being channelled or furrowed and velvety, whilst the pyloric portion is smooth. It is in the fundus only where true gastric juice, viz., pepsin and acid, is

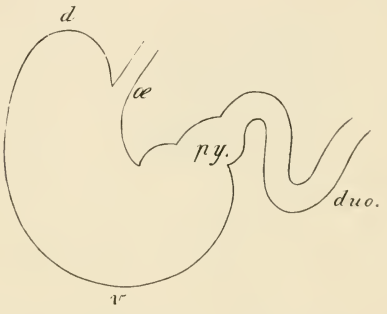


Fig. 8.—Longitudinal Section of the Stomach of the Horse, showing the Syphon Trap of the Duodenum.

œ., œsophagus; *py.*, pylorus; *d*, left sac; *r*, fundus; *duo.*, duodenum.

secreted, in the smooth pyloric mucous membrane only pepsin is formed, but this will be fully dealt with presently. The area of the membrane of the fundus-secreting surface is about one foot square. Fig. 7 shows the relative position of the various parts of the mucous membrane of the stomach of the horse. The drawing accurately indicates the shape of the stomach, the position of the inlet and outlet, and the direction and position of the various areas.

A very remarkable amount of mucin is secreted by the

villous sac of the stomach, which forms over the surface of the viscus a thick gelatinous firmly adherent coating like white of egg, which cannot be washed away even by a powerful jet of water. We shall later draw attention to its functions.

The pyloric orifice of the stomach is usually large and open, the cardiac is tightly closed; these two openings are situated close together. There is a distinct pyloric ring, behind this the duodenum is dilated, and the gut here comports itself in such a singular manner (which has a very important bearing on the pathology of the organ) that mention must be made of it here. From the pylorus the duodenum curves down at once and then up again, forming a letter U; so much does this remind one of a well-known form of trap used in drainage, that I have described it as the syphon trap of the duodenum (Fig. 8). The use of this trap appears to be to regulate the passage of material from the stomach into the intestines. I have shown that its presence in all probability influences rupture of the stomach, for the more distended the large bowels become, the greater the pressure exercised on the duodenum, and in cases of severe tympany the passage from the stomach to the intestines is completely cut off; as fermentation still continues in the stomach, and the material can neither escape forwards into the œsophagus, nor backwards into the bowel, the coats of the viscus are completely lacerated through the intense strain.

The physiological points of interest in the structure of the horse's stomach are: 1, its small size; 2, not being in contact with the abdominal wall, but resting on the colon; 3, the outlet and inlet situated close together; 4, the contracted cardia; 5, only a portion of its surface being capable of secreting a digestive fluid; 6, the remarkable differences in its mucous membrane.

We must now return to the points which we have previously stated as possessing an important influence on the process of gastric digestion.

The length of time food remains in the stomach will depend upon its chemical composition and bulk, also as

to whether more than one kind of food is partaken of at the same time; bulky food, such as hay, passes out more rapidly than condensed food, such as oats. Oats contain considerably more nitrogenous matter than hay, therefore a longer period must be devoted to their digestion in the stomach; we will, therefore, consider first of all the digestion of hay, then that of oats.

Digestion of Hay.—Hay, as we have shown, mixes in the mouth with four times its bulk of saliva, and after a very perfect grinding passes into the stomach; assuming the stomach to be empty, it passes at once to the right side; the gastric juice begins to act, and, as before described, chyme commences to pass into the intestines probably in a very imperfectly elaborated form. Assuming the animal to have finished the hay, we now find the output into the intestine becomes small and slow; the gastric juice has an opportunity of acting upon the ingesta, which turns yellow on that surface in contact with the stomach-wall; the compression of the latter on the contents causes them to become distinctly moulded into a mass, the shape of the stomach, being more fluid towards the pylorus than elsewhere. The greater curvature in all probability is fuller than the lesser. The material is perfectly comminuted, and resembles firm, dry, green and yellow fæces, and the smell is peculiar, like sour tobacco.

The yellowness is due to the gastric juice, and is consequently more marked towards the pylorus; the portion coloured green is the part as yet unacted upon by the juice. The total surface of the stomach and its contents are now acid, though Colin says otherwise. The acidity is greater at the fundus than at the cardia. This acidity shows that a diffusion of the gastric juice must have been going on. There is no evidence of any churning motion, the cake-like condition into which the hay is compressed in spite of its four equivalents of saliva is due to the compression of the material by the stomach walls.

The duration of stomach digestion of hay is variable, but I quote one or two of Colin's experiments. A horse

received 5½ lbs. of hay, which he took two hours to eat; at the end of that time he was destroyed, and the stomach contained 2·2 lbs.; thus in two hours he had digested 3·3 lbs. Another horse received 5½ lbs. hay, and was destroyed three hours from the time of commencing to feed; in the stomach was found 1·54 lbs.; in three hours he had digested 3·96 lbs.; in the third hour (during which time he was not feeding), judging from the first experiment he had digested only ·66 lb., whereas the previous rate of digestion for the first two hours was at the rate of 1·65 lbs. per hour. To return to our previous statement, when the animal is no longer feeding the rate of digestion at once becomes reduced, and it is probable that several hours must elapse, assuming no further food be given, before the stomach completely empties itself. This period may be fifteen, eighteen, twenty-four to thirty-six hours.

I starved a horse for twenty-four hours, and at 6 a.m. gave him 6 lbs. of dried grass; he was destroyed at 3 p.m., and the stomach still contained 2½ lbs.; in nine hours, therefore, only 3½ lbs. had been digested. In another observation carried out under similar conditions, only 1 lb. had been digested in four hours and three-quarters. Of 4 lbs. hay given only 1 lb. 11 ozs. was digested in six hours; of 3½ lbs. hay, 2¼ lbs. were digested in five and a half hours, and of 4 lbs. hay, 2 lbs. 12 ozs. were digested in five hours.

Colin's elaborate researches furnish us with very complete data on the question of hay digestion in the horse. He fed fourteen horses on hay, and destroyed two of them at regular intervals; each animal received 5·5 lbs. of hay, and digestion was counted from the time they were fed. Here are the results:

Amount of Hay given, 5·5 Lbs.

				lbs.		*lbs.*
After 2 hours,	the first horse had digested			3·37;	the second,	3·08
„ 3	„	„	„	3·83	„	4·24
„ 4	„	„	„	4·04	„	3·56
„ 5	„	„	„	4·32	„	5·03
„ 6	„	„	„	4·10	„	4·55
„ 7	„	„	„	4·01	„	4·35
„ 8	„	„	„	4·87	„	4·44

We observe that the rate of digestion during the first two hours is rapid, and it then falls off, so that even at the end of eight hours there is still something left in the stomach. The second horse in the five hours' observation had very nearly digested the whole of the ration, but this is an exception.

There is no doubt that it is extremely difficult to get the stomach to empty itself. I fed a horse on dried grass and destroyed it eighteen hours later; there was still a small quantity of food in the stomach. In another case the stomach, after fifteen hours, was found empty. In a third case a horse was given grass twice at intervals of twenty-four hours. He was destroyed eighteen hours after eating his last feed, and a handful of grass was still found in his stomach.

Digestion of Oats.—We must now consider the digestion of oats, and here we observe the same remarkable fact noted under hay, viz., that the stomach commences to pass its contents into the intestine during feeding, and that this considerably slackens when no more food is entering the viscus. Colin fed six horses on 5·5 lbs. of oats each, and destroyed them at certain intervals.

				lbs.			*lbs.*
After	2	hours,	one horse had digested	2·728	; a second,		2·5564
,,	4	,,	,,	3·095	,,		3·4562
,,	6	,,	,,	3·553	,,		3·0250

I have observed in a horse which had received 2 lbs. of oats, and was destroyed twenty hours later, that the stomach had not completely emptied itself; in another experiment four hours after feeding on 1 lb. of oats, I recovered 6 ozs. from the stomach.

A horse received	And was destroyed in	Amount digested,
lbs. oats.	*hours.*	*lbs. ozs.*
4	4	2 3
3	$4\frac{1}{2}$	1 $11\frac{1}{4}$
4	4	2 4
3	$3\frac{3}{4}$	2 $2\frac{1}{2}$
3	4	—
4	4	1 $13\frac{1}{2}$
3	$6\frac{1}{2}$	2 $6\frac{1}{2}$
4	4	3 0
4	4	0 12

I include the last horse to illustrate a point of some little importance in the feeding of animals. For eighteen months

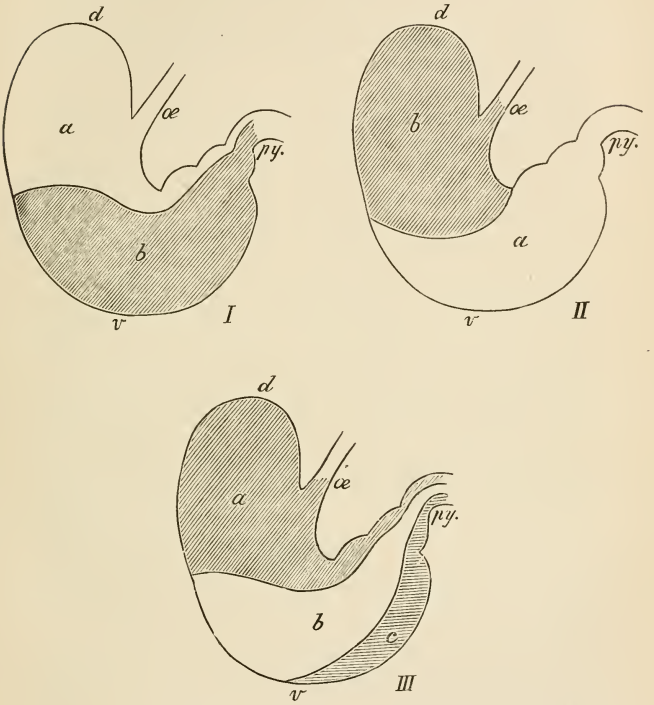


FIG. 9. — LONGITUDINAL SECTION OF THE HORSE'S STOMACH, SHOWING THE ARRANGEMENT OF THE FOOD ACCORDING TO THE ORDER IN WHICH IT WAS RECEIVED.

In each case *œ.* is the œsophagus, *py.*, pylorus ; *d*, the left sac ; *v*, the fundus. *I.* Hay first, followed by oats : *b*, the hay ; *a*, the oats ; the latter are passing along the lesser curvature and escaping with the hay at the pylorus. *II.* Oats first, followed by hay : *a*, the oats ; *b*, the hay. *III.* The order of three successive feeds : *c*, the the first feed ; *b*, the second ; *a*, the first (Ellenberger).

this horse had never tasted corn, having been fed on a patent food ; a sudden change in diet is the explanation

why it only digested 12 ozs. of oats in four hours. It will be observed that the fifth horse in this series digested nothing, even at the end of four hours; I can only account for this by the animal being in a strange place where the feeding experiment was carried out, and being of a very nervous disposition.

Arrangement of Food in the Stomach.—An interesting practical and physiological study is the effect of feeding horses on different foods in succession. When hay is given first and oats afterwards, the hay is found close to the greater curvature and pylorus, and the oats in the lesser curvature and cardia. No mixing has occurred; both aliments are perfectly distinct, and a sharp line of demarcation exists between them (Fig. 9, I.). The presence of the oats, however, has caused the hay to pass out more rapidly than it would have done had it been given alone. Colin observed that half the hay, but only one-fourth or one-sixth of the oats, would, under these conditions, pass into the intestine in two hours. During digestion a mixing of these foods occurs at the pylorus, but nowhere else. Ellenberger has shown that when hay and oats are given in this order, a portion of the oats may pass out into the bowel by the lesser curvature without entering either cardia or fundus of the stomach (see Fig. 9, I.). No matter what compression the contents have undergone as the result of gastric contractions, the foods always remain distinct.

When oats are given first, and followed up by hay, the oats commence to pass out before the hay; but the presence of the hay causes the oats to pass more quickly into the intestines (Fig. 9, II.).

We may summarise these facts by saying that in a succession of foods the first taken passes out first; that does not mean to say that the whole of it passes out before any portion of the succeeding food enters the bowel, for we have shown that after a time at the pylorus they mix and pass out together; but the actual influence of giving a food first is to cause it to pass out first. The practical deduction is that, when foods are given in succession, the least albuminous

should be given first. This appears to distinctly reverse the English practice of giving oats first and hay afterwards, but perhaps only apparently so, for experiment shows that the longer digestion is prolonged, the more oats and the less hay pass out, so that some hay (under ordinary circumstances a considerable quantity) is always left in the stomach until the commencement of the next meal. Now, the presence of this hay from the previous feed may prevent the corn of the succeeding feed from passing out too early. Ellenberger says that in order that horses may obtain the fullest possible nutriment from their oats, hay should be given first *and then water*, which carries some of the hay into the bowel; after some time the oats are to be given. The hay now passes into the bowel, and the oats remain in the stomach. This will hardly fit in with our English views of feeding and watering.

If a horse be fed on three or four foods in succession, they arrange themselves in the stomach in the order in which they arrived, viz., they do not mix; the first enters the greater curvature, the last the lesser curvature, and it is only at the pylorus that any mixing occurs under ordinary conditions (Fig. 9, III.).

This regular arrangement of the food in layers, when taken in succession, is only disturbed when a horse is watered after feeding; under these circumstances the contents are mixed together and digestion thereby impeded. Apart from this, the ingestion of a considerable quantity of fluid into a stomach already containing as much as it should hold, means that material is washed out of the stomach into the small intestines, and this sets up irritation and colic. In this way more than half the food may be washed at once out of the stomach. The water which a horse drinks does not remain in the stomach, but passes immediately into the small intestines, and in the course of a few minutes finds its way into the cæcum; hence we have the golden rule of experience that horses should be watered first and fed afterwards.

The **appearance of the food in the stomach** depends upon

the period of digestion; we have previously drawn attention to the fact that an hour or two after hay has been taken, the material is found in a finely chopped condition, firm, one may almost say dry in places, though towards the pylorus it is liquid. This hay contains between four and five parts of saliva; is yellow in colour where the gastric juice has attacked it, but rather of a greenish tint elsewhere. It has a peculiar odour. Some hours after a feed the stomach is found to contain a variable quantity of watery fluid discoloured by the hay which is left behind, part of which may be found floating on the fluid. At other times, when the stomach is empty, the fluid is viscid, contains numerous air bubbles, and is of an amber or yellow tint. This particular fluid is no doubt saliva and mucin, with possibly a little bile.

When oats alone have been given the contents of the stomach are found liquid, the fluid being creamy in consistency and colour; the oats are swollen, soft, and their interior exposed. Towards the end of digestion the creamy fluid is replaced by the frothy yellow one. With both hay and oats, and also other foods, there is a peculiar sour-milk-like smell from the contents of the stomach, more marked with bran and oats than with hay, which, as previously mentioned, smells like sour tobacco.

The **reaction of the contents of the stomach** is strongly acid; this acid reaction may be obtained on the cuticular as well as the villous portion of the viscus, and is very persistent: the cuticular membrane even after prolonged washing gives an acid reaction. The acidity is derived entirely from the juice secreted by the villous membrane of the fundus.

My observations on this subject do not agree with those of Ellenberger, who says that during the first hour of digestion the stomach may be alkaline; acidity then commences in the fundus and extends to the cardia, though for some time the proportion of fundus acidity is three or four times greater than that of the cardia; in the course of five or six hours the proportion of acid throughout the stomach is equal.

When the stomach is empty, as after a few days' starvation, its reaction is neutral or alkaline. I have observed extreme alkalinity towards the pylorus under these conditions, due no doubt to the regurgitation of bile and pancreatic fluid.

The Stomach Acids.—It is not necessary here to enter into a long discussion on the nature of the gastric acids. Both in the horse and man a considerable amount has been written to prove that the acidity depended upon lactic or hydrochloric acids. It is possible that both these views may be reconciled. Ellenberger and Hofmeister are of opinion that immediately after a meal lactic acid predominates in the horse's stomach, to be replaced by hydrochloric at about four or five hours from the commencement of feeding. These observers found that the nature of the acid depends upon the region of the stomach, the period of digestion, and the nature of the food, oats inducing an outpouring of hydrochloric acid, whilst hay favoured the organic acids, as seen in the following table :

	Total Acid.	*Hydrochloric Acid.*	*Lactic Acid.*
On a diet of chopped straw and oats -	·045%	·0163%	·0287%
On a diet of oats - - -	·110%	·049%	·061%
On a diet of hay - - -	·182%	·002%	·179%

In the contents of the stomach, hydrochloric, lactic, butyric and acetic acids may be found, the two latter in insignificant quantities only. In flesh feeders HCl predominates 2·5 per 1,000, and lactic, in small quantities, ·07 per 1,000. In grain feeders lactic acid at first predominates, and later HCl in small quantities. Lactic acid exists throughout the whole stomach, but predominates in the right and left sacs, whilst hydrochloric acid principally exists in the fundus region. Lactic is the first digestive acid employed, but towards the end of digestion hydrochloric exists throughout the whole stomach. The amount of lactic acid found in the stomach of the horse during the first hours of digestion is considerable, amounting to $1\frac{3}{4}$ ozs. or even as much as $3\frac{1}{2}$ ozs. (Ellenberger).

Having gone very carefully into the question of the presence of hydrochloric and organic acids in the stomach contents, I can only say that, no matter at what period of digestion I have made the observation, I have never yet succeeded in finding hydrochloric acid in the stomach of the horse, and I am convinced that lactic is the chief, if not the sole, digestive acid in this animal.

The **Secretion of Gastric Juice** is accomplished in certain glands, known as the gastric glands. In man these are divided into cardiac and pyloric glands, each having not only a different structure, but a distinct function. In the horse cardiac glands are impossible, owing to the presence of the cuticular coat; but it has been shown that the villous coat contains glands corresponding to cardiac, which are principally situated in the greater curvature, not far from the margin of the cuticular coat, and extending over a comparatively small area, described on p. 112 as not larger than 1 foot square, this portion of the stomach being known as the fundus (Fig. 7). Mucus is secreted in large quantities by the villous coat of the horse's stomach, and is formed principally in the fundus. This mucus is secreted by the epithelial cells lining the villous coat and the upper portion or outlets of the gastric glands.

The two kinds of gland employed in the production of gastric juice are both found in the villous coat, the one in the fundus, the other in the pyloric portion. They are simple or divided tubes lying side by side, and opening generally in groups on the surface of the mucous membrane by means of a shallow depression in the coat, which can readily be seen studded over the tunic of the fundus, giving it a rough appearance owing to the elevation of the mucous membrane between the openings of the glands, whilst in the pyloric region the membrane is as smooth as that found in the intestine. Each gland consists of a body, neck, and mouth, and is lined with cells. It is in respect of the cellular contents that the so-called pyloric and fundus glands differ.

The cells of the fundus glands are small, polyhedral,

granular, and nucleated; those which line the lumen of the gland are called the principal cells. Scattered amongst the principal cells, but existing in larger numbers at the neck of the gland than at its base, are found certain large cells (oval, granular, and nucleated), which from their position relative to the lumen of the gland are called parietal, marginal, or border cells. These cells are distinctive of the fundus glands, and they stain readily with aniline blue.

The pyloric gland has below its neck but one variety of cell—viz., the cylindrical—containing a nucleus at its attached edge. The duct is lined above the neck by the ordinary epithelium of the stomach, and the same remark applies to the cardiac glands; it is from this epithelium that the mucus is secreted. Lying deep in the mucous membrane of the stomach between the gastric glands may be found large mucus secreting glands, which, doubtless, contribute to the formation of the remarkable amount of mucin found in the stomach of the horse.

The difference in the structure of the follicular glands of the stomach depends upon their function. The important distinction between the fundus gland with its principal and parietal cells, and the pyloric gland with its principal cells only, is that the former secretes both the pepsin and acid of the gastric juice, the acid being separated from the blood, or secreted, by the parietal cells, whilst the pepsin only is formed by the principal cells; the pyloric glands, on the contrary, only secrete pepsin and no acid.

Ellenberger states that he has found fundus glands in the pyloric region.

We have previously mentioned that the cells of the salivary glands undergo certain changes in appearance, the result of rest and activity; the same remark applies to the gastric follicles. These changes have been worked out by Heidenhain and Langley. The former found that the large marginal cells of the fundus glands during activity—viz., digestion—bulged from the side of the gland and encroached on the lumen, and also became much larger than ordinary; the principal cells of the gland were found as

the result of digestive activity to become very granular. The active pyloric cells also became more granular, and the nuclei left the base of the cell and worked towards the centre of it. During hunger the chief cells of the fundus glands are clear and large, the parietal cells small.

No doubt the appearance presented by the secretory cells depends upon the method by which they are prepared for examination. Langley has therefore, by another method of inquiry, given an opposite description of the active and passive cells of the gastric glands. He found that in the active state the granules decreased in number, the cells becoming clear, and being capable of differentiation into a clear outer and a granular inner zone, just as we have seen in the parotid gland. During rest the entire cell became granular. The parietal cells were found to increase in size, but did not become granular.

Gastric Juice of the horse has not been obtained pure. The experiments made by Tiedemann and Gmelin of introducing foreign bodies into the stomachs of horses did not lead to a pure secretion, owing to the amount of saliva swallowed. The following table, constructed by C. Schmidt, represents the composition of this juice in man, the dog, and sheep:

	Man.	*Dog.*	*Sheep.*
Water	994·40	973·06	986·14
Organic matter	3·19	17·13	4·05
Sodium chlor.	1·46	2·50	4·37
Calcium „	·06	·26	·11
Hydrochloric acid	3·19	17·13	4·05
Potassium chlor.	·55	1·12	1·52
Ammonium „		·47	·47
Calcium phosph.	·125	1·73	1·18
Magnesium „		·23	·57
Ferric „		·08	·33

The following table from Ellenberger* gives an analysis of the so-called gastric juice of the horse, and also of the

* *Op. cit.*

stomach-fluid after feeding on different foods; in connection with the latter, it is to be remembered that the fluid consists of the soluble, organic, and inorganic portions of the food, mixed with saliva, and gastric juice:

		Stomach-fluid after feeding on		
	Gastric Juice.	*Oat Straw.*	*Oats.*	*Hay.*
Water - -	982·8	843·4	925·0	972·6
Organic matter -	9·8	69·9	40·0	20·2
Inorganic matter	7·4	86·7	35·0	7·2
Hydrochloric acid	1·3	—	—	—

Gastric juice is acid in reaction, clear when filtered, slightly yellow in the horse, brownish in sheep, with a specific gravity of 1010. A remarkable peculiarity of the gastric juice of flesh feeders is the power it possesses of resisting putrefaction. This is not the case with the horse. Examined by the polariscope, gastric juice turns the ray of polarized light to the left. The effect of reagents on the secretion shows that acids produce no precipitate, whilst alkalies do, and that alcohol produces a heavy precipitate, which is in part due to the ferments found in the fluid. The amount of salts present is about ·7 per cent. or ·8 per cent.

The acidity of the gastric juice we have before spoken of, it only remains to speak of the ferments—viz., pepsin and rennin—and of the substance known as mucin.

Pepsin is a body allied to proteids, which by appropriate methods can be obtained in the form of a yellowish powder, soluble in water, insoluble in alcohol; it does not give all the tests characteristic of the proteid group of bodies. The ferment is secreted in the principal cells of the fundus and pyloric glands, but exists in them, not in the form of pepsin, but as its immediate precursor, pepsinogen. There is no pepsin secreted by the cuticular or left sac of the stomach of the horse, and Ellenberger considers that even the pyloric region contains no ferment during the first hour of digestion.

It is found that if pepsin be obtained in a pure con-

dition it produces no action on food. It is essential to its function that it should be associated with an acid, which the majority of observers regard as hydrochloric. In this condition it readily acts on proteids, converting them into peptones. This function is spoken of as peptonizing.

Pepsin may be destroyed by heat. It loses its activity at 134° to 136° F., though in the dried state it may be raised to 212° F. without being destroyed. It best manifests its activity at a temperature of 104° F.

Pepsin is described as a ferment, inasmuch as, besides splitting up the proteid substances of food, one of its leading characteristics is that a very small amount of it is capable of performing a considerable amount of work. It is probable that so long as it is acting in an acid medium it is not appreciably used up.

The **Rennin,** or milk-curdling ferment, is also formed in the same cells as the pepsin; it is destroyed at a lower temperature than pepsin. By means of magnesium carbonate the two ferments may be separated.

The action of rennin is to clot the casein of milk. This process is used in the manufacture of cheese, an infusion of the mucous membrane of the stomach being sufficient to set up this action in the milk. The ferment acts without the presence of an acid, but it is essential in order that the rennin may clot casein that calcium phosphate should be present.

In the fourth stomach of the calf and sheep this ferment may be readily found, and it has been said to exist in the stomach of the horse.

A third or **lactic acid ferment** has been described as existing in the gastric juice, which has the power of converting milk-sugar into lactic acid. Dilute caustic soda, which will destroy both pepsin and rennin, has no effect on this ferment.

Mucin.—The remarkable amount of mucin in the stomach of the horse is secreted by epithelial cells and mucous glands, as previously mentioned. How much mucin is formed, independent of the gastric juice, we have no means

of knowing; all we know is that it is less during hunger than during digestion, and is less in ruminants than in horses.

We have no knowledge of the nerves governing the secretion of gastric juice.

The **action of the gastric juice** is directed solely against the proteid principles of the food. There are other changes, no doubt, besides peptonizing occurring in the stomach, but these are independent of the gastric juice, and are perhaps, in some cases, inhibited by it.

Gastric juice converts albumins into **Peptones.** This change occurs whether an animal or vegetable proteid be given. The conversion is not a direct one, as between albumins and peptones occur the intermediate products albumoses.

It is well known that albumins cannot pass through an animal membrane, whereas the distinctive character of peptones is their power of dialysing, which enables them, no doubt, to pass readily into the absorbent vessels of the intestines.

The amount of peptone at first produced is small; especially is this the case early in digestion, for, as we shall presently show, according to Ellenberger, peptic digestion is the second stage of stomach digestion in the horse.

The amount of peptone in the stomach is stated by the same observer to be smaller in the left half of the stomach than in the right; according to my experience peptone disappears as soon as it is formed, for I have never succeeded in finding any in the stomach of the horse.

But the gastric changes are not quite so simple as would at first sight appear. Experimental inquiry shows that peptones are obtained in two forms, one remaining stable and undergoing no further change, whilst the other may, under the influence of one of the ferments of the pancreatic juice (trypsin), be split up into leucin and tyrosin, two amido acids which will engage our attention later on.

All peptones which yield as further products leucin and tyrosin are termed **hemi-peptones**, whilst those which do not are called **anti-peptones.**

This remarkable difference indicates that the proteid molecule may consist of two parts, an anti and hemi portion yielding respectively anti-albumose and anti-peptone, and hemi-albumose and hemi-peptone.

Much confusion has occurred through the difference in the nomenclature adopted by various observers in describing these different products. The one most generally employed is that of Kuhne's, given above, and here tabulated:*

Albumin.

Hemi-albumin.	Anti-albumin.
Hemi-albuminose.	Anti-albuminose.
Hemi-peptone.	Anti-peptone.

Amylolytic Changes.—We have referred to other changes occurring in the stomach independently of peptonizing. There can be no doubt that starch is converted into sugar; all the sugar I have found in the stomach could not have been converted in the mouth, considering the feeble action of horse's saliva. Assuming, however, that the saliva assists, we know from the researches of Ellenberger and Hofmeister that it can convert starch into sugar even in the presence of 2 per cent. lactic acid; whilst it ceases in the presence of ·5 per cent. hydrochloric acid. The whole of the starch, however, is not converted in the stomach, for some may be distinctly found in the early part of the small intestines.

Ellenberger and Hofmeister are of opinion that starch conversion in the stomach of the horse occurs not only through the saliva swallowed, *but by the development of ferments from the food;* they found that oats could yield a starch-converting ferment active at the body temperature, but destroyed by boiling; they have further stated that starch-converting ferments may in the horse be derived from the air swallowed with the food.

The view I hold as to the means by which the starch is converted into sugar by the horse is as follows:

* Copied from Halliburton.

Starch is not converted in the mouth, but it is in the stomach by means of a starch-converting ferment *contained in the oats*, which is capable of acting in the presence of lactic acid. My observations on this subject are incomplete, and therefore unpublished.

After this, and with what we have to say on the cellulose ferment, we need seek for no other explanation of the reason why oats are so universally adopted as food for horses.

According to Ellenberger, starch is the first substance digested in the stomach of the horse, a diastatic ferment existing in the left inert sac, and also in the fundus.

Starch when attacked by a diastatic ferment is first converted into soluble starch, then into dextrin, and lastly into sugar; part of the starch may be converted into lactic acid by lactic fermentation.

Fats are not acted upon in the stomach, though the envelope surrounding the fat globule is digested, and the fat set free.

Milk is curdled in the stomach by means of the rennin; the casein thus produced is converted into peptones in the ordinary manner.

Cellulose fermentation is considered by Tappeiner to occur in the left sac of the stomach, and when marsh-gas has been found in this organ, it results from cellulose decomposition. Ellenberger lays no stress on these results, but recently Brown* has shown that the destruction of the cell-wall of oats and barley occurs in the stomach, where it is dissolved by a cyto-hydrolytic ferment *pre-existent in the grain*. The changes occur with extraordinary rapidity in the stomach of the horse. The researches of this observer on a cellulose-dissolving ferment are of the greatest interest to the veterinary physiologist, and of considerable practical importance.

The Various Periods of Stomach Digestion.—From what has been previously said, it will be seen that digestion in the stomach of the horse may be divided into certain

* 'On the Search for a Cellulose-dissolving Enzyme,' H. J. Brown, F.R.S., *Journal of the Chemical Society*, 1892, p. 352.

periods, the existence of which has been determined by Ellenberger and Hofmeister, whose views are here given :

First period : lasts but a short time, during which starch is converted into sugar, accompanied by lactic fermentation.

Second period : during this starch is principally converted into sugar in the left sac, and a small quantity of proteid is converted into peptone in the fundus; the acids present are lactic in the left, and a little hydrochloric in the right sac.

Third period : one of mixed digestion; both starch and proteid conversion occurs—the former in the pylorus, the latter in both fundus and pylorus. The acid present is principally hydrochloric.

Fourth period consists of pure proteid digestion; no starch conversion can occur owing to the universal presence of hydrochloric acid. It is impossible to state definitely the length of these various periods, for so much depends upon the presence of fresh food in the stomach. Where the interval between the meals is considerable, the periods extend over several hours; and in all cases they run into one another. Had it not been for the weight of Ellenberger's authority, I should not have considered it necessary to have mentioned the various periods given above.

After a moderate feed digestion is at its height in 3 or 4 hours.
„ full „ „ „ „ 6 to 8 „
„ an immoderate „ „ delayed still longer.

Gastric Digestion of Ruminants.—Ruminants are described as having four stomachs—viz., the rumen, reticulum, omasum, and abomasum. Physiologically considered, there is but one stomach—viz., the abomasum; the others may be regarded as œsophageal dilatations.

The **Rumen** is of enormous size, capable of holding 60 gallons; it is divided into certain sacs, has a well-developed mucous membrane, which in part is covered by leaf-like papillæ, the glands are small and unimportant, and contribute no digestive fluid. The muscular fibres of the wall are distinctly striated, which is a remarkable

circumstance, and probably connected with the function of rumination. The contents of the stomach are alkaline, excepting in calves fed on milk, and consist of food only roughly comminuted, containing an amount of fluid which plays an important part in rumination, and which is derived from the fluid consumed, mixed with enormous quantities of saliva. This stomach communicates with the œsophagus and the reticulum.

The **Reticulum** is arranged like a honey-comb; it is a very small stomach, and its contents are normally fluid and alkaline. In the pouches formed by the reticulated arrangement foreign bodies are commonly found, and when they penetrate the heart it is from here that they pass into the chest.

The use of the reticulum is to contain fluid; so that the openings leading from this stomach into the cavities of the first and third are considerably above the base of the viscus. This fluid is used during rumination, and is forced into the œsophagus by muscular contractions. In reaction the second stomach is alkaline, and it possesses no secretion from its walls.

The muscular coats of the stomachs vary in thickness. The rumen is comparatively thin, the reticulum thick. By means of the muscular tissue the food is submitted to a constant churning motion, which continually revolves the contents. This process in the rumen is one of considerable importance, as it brings the food towards the opening of the œsophagus for the purpose of rumination, The process is slow and deliberate, the material at the posterior portion of the rumen being gradually forced forward and upward, and made to revolve within the cavity.

Solid material, no doubt, enters the rumen and reticulum first, but liquids may enter all four stomachs at one and the same time; this has been proved by the investigations of Flourens. It is probable that the greater part of the fluid drunk passes direct to the rumen and reticulum, for it is certain that the presence of fluid in these stomachs is absolutely essential to rumination.

The food which newly arrives in the stomach mixes at once with that already there, and undergoes, in the presence of saliva and the water consumed, a peculiar maceration which suits it for remastication. Cellulose is also digested in the rumen through the presence of ferments, and the amount of conversion which can thus occur has been estimated at between 60 per cent. and 70 per cent.

Ellenberger's views on the function of the rumen and reticulum are as follows:

In the rumen the food is mechanically divided through the motion of the walls of the organ, and a thorough incorporation occurs; owing to the quantity of fluid found in this stomach, softening and maceration of the food substance takes place; carbo-hydrates are digested through ferments contained in the food itself; in this way starch is converted into sugar, cane-sugar into maltose, and cellulose, especially in the sheep, undergoes decomposition; further, proteids are slowly converted into peptones through food ferments, not through a true peptic ferment; the rumen is the seat of fermentation and gas production.

The reticulum has the same function as the rumen, and it regulates the passage of food from the first to the third stomach, and from the first stomach into the mouth.

In young ruminants digestion principally occurs in the fourth stomach, as the others are almost rudimentary. It is remarkable, however, how soon they develop, and how easily the process of remastication is acquired in young animals placed on solid food.

The **Omasum**, or third stomach, is peculiar. Its physiology has been elaborately worked out by Ellenberger. This authority says that it possesses no secreting power, that its function is to compress and triturate the food, which it crushes between its powerful muscular leaves, and rasps the ingesta down by means of its papillæ. The contents of this stomach are always dry, due to the fluid portion being squeezed off and flowing into the fourth stomach by the action of gravity and the pressure exercised by the viscus. Normally it possesses no reaction; if found acid, it is due to

regurgitation from the fourth stomach. The third stomach has a separate source of nerve supply. Irritation of the pneumogastric produces contraction of all the other stomachs but this one.

In the **Abomasum**, or fourth stomach, true digestive changes occur. The acid secretion, formed in the manner before described, converts the proteids into peptones, this change being more active at the cardia than at the pylorus. Ellenberger states that in the abomasum the digestion of starch is the first to take place, and then proteid digestion.

In the fourth stomach of the calf a milk-curdling ferment exists.

Stomach digestion in the **Pig** has also been worked out by Ellenberger and Hofmeister. The stomach of the pig is peculiar: it is a type between the carnivorous and ruminant, and is divided by the above observers into five distinct regions, which do not all possess the same digestive activity.

The gastric juice of the pig contains for the first hour or two of digestion lactic, and afterwards hydrochloric, acid; pepsin is present, and a ferment which converts starch into sugar.

The remaining points in gastric digestion in the pig, viz., the various periods of digestion, the changes in the acid, and the slowness with which the viscus empties itself when no fresh food is given, are identical, strange to say, with those of the horse.

Absorption from the Stomach.—The needful changes having occurred in the stomach, and I now refer principally to the stomach of the horse, our next step is to inquire into the proportion of food so altered as to be fit for absorption.

Experiment shows that in the stomach 40 to 50 per cent. of the carbo-hydrates of the food have been converted into sugar; whilst 40 to 70 per cent. of the proteids are converted into peptones. Where food has been long in the stomach, not more than 2 to 10 per cent. of the proteids pass out unacted upon; but under ordinary circumstances we cannot count upon a larger digestion of proteids than 40 per cent.

In ruminants probably the greater part of the food substance is acted upon in the stomachs, leaving comparatively little for the intestines to perform.

In spite of the changes which occur in the stomach, it has been proved by the experiments of Colin that *no absorption occurs from this organ in the horse.* It would be useless to recapitulate all his experiments. They were generally performed with strychnine, and he found that so long as the pylorus was securely tied, no symptoms of poisoning would occur when the alkaloid was introduced into the stomach no matter how long it was left there, but that when the ligature was untied, and the contents of the stomach passed into the intestines, poisoning rapidly followed. These remarkable results were obtained by him so often, and under such varying conditions, as to leave no doubt as to the accuracy of the observations. We can only surmise, therefore, that no absorption of sugar or peptones occurs in the stomach. It is certainly very remarkable what becomes of the peptones. I have never found any in the stomach contents, no matter what the period of digestion may be; and if they are not absorbed in the stomach, they must pass very rapidly into the intestines and enter the vessels at once, as no peptone can be found in the small intestines.

I am not at all prepared to explain this non-absorption from the stomach of the horse, and will touch on it later. Colin attributes it to the small area of the mucous membrane, which, he says, cannot be secreting gastric juice and absorbing at the same time; and in the empty stomach he attributes the non-absorption of poisons to the thick layer of tenacious mucus, which we have previously mentioned covers the villous stomach of the horse.

Self-digestion of the Stomach.—A question which has for a long time given rise to an energetic discussion, is the reason why the stomach during life does not digest itself, seeing that the action of its secretion is so potent that portions of living material, legs of frogs, ears of rabbits, etc., if introduced into it are readily digested, also that post-mortem

digestion of the stomach in some animals is far from rare. No perfectly satisfactory solution of the problem has yet been afforded; the alkalinity of the circulatory blood is not considered to meet the difficulty. In an extensive post-mortem experience amongst horses, I have never yet met with post-mortem digestion of the stomach. Whether this is due to the horse's acid being mainly or wholly lactic, I cannot say.

The Gases of the Stomach.—The nature of these largely depends upon the food; traces of oxygen, a quantity of carbonic acid, and variable amounts of marsh-gas, sulphuretted hydrogen, hydrogen, and nitrogen are found. The oxygen and nitrogen are derived from the swallowed air; the carbonic acid is derived from the fermentation of the food, and the action of acids on the saliva; and the marsh-gas is obtained by the decomposition of cellulose.

Tappeiner found the following gases in the stomach of the horse:

Carbonic acid	75·20	67·73
Oxygen	·23	·00
Hydrogen	14·56	12·66
Nitrogen	9·99	19·54

I have found in the stomach of a horse in perfect health, which had been fed on oats, the following gases in every 100 volumes:

Carbonic acid	21·2
Oxygen	11·8
Hydrogen	5·6
Nitrogen	61·4

but I take it that the proportion of these gases must vary considerably, and depend largely on the diet.

In cattle, by feeding on hay, the following gases were found by Tappeiner in the rumen:

Carbonic acid and sulphuretted hydrogen	65·27
Hydrogen	·19
Marsh-gas	30·55
Nitrogen	3·99

Vomiting.

Vomiting amongst solipeds and ruminants is rare, and I doubt whether in the former animal it should not be considered rather as a pathological than a physiological phenomenon.

The reasons given why the horse cannot vomit are various: (1) The thickened and contracted cardiac extremity of the œsophagus; (2) the oblique manner in which this latter enters the gastric walls; (3) the dilated pylorus lies close to the contracted cardia, so that compression of the stomach contents forces them into the duodenum; (4) the cuticular coat is thrown into folds over the opening of the cardia; (5) encircling the cardia are muscular loops the contraction of which keeps the opening tightly closed; (6) the stomach is not in contact with the abdominal wall. All these and other reasons have been assigned as the cause of non-vomiting in the horse; yet on turning to ruminants, which normally do not vomit, we find these conditions reversed. The stomach or stomachs and œsophagus freely communicate, the largest stomach lies in contact with the abdominal wall, the cardia is freely open, the œsophagus of great size, and, still stranger, the animal has the ability under the control of the will to bring up food from the stomach as a normal condition, and yet no vomiting occurs.

It is evident, therefore, that all these theories are not sufficiently satisfactory to account for the absence of vomiting, and we are bound to suppose that the vomiting centres in the medulla of both horse and ox, are either only rudimentary or very insensitive to ordinary impressions.

Vomition in the horse is no doubt seriously interfered with by the thickened cardia and the arrangement of the muscular fibres; the folds of mucous membrane filling up the orifice I do not think could offer a serious obstruction to a distended stomach, for we know that even when this membrane is dissected away post-mortem, a stomach will burst rather than allow fluid or air to be forced from the

pylorus through the cardia, until the muscular fibres surrounding it are partially divided.

Vomition in the horse is generally indicative of ruptured stomach, and much has been written as to whether vomiting occurs before or after the rupture. From no inconsiderable experience in these cases, I have arrived at the conclusion that it may occur at either time. I am convinced that a horse may vomit though a rent seven or eight inches long exists in the stomach walls.

Dilatation of the cardia is the great inducement for vomiting to occur in the horse, and in every case examined post-mortem where vomiting occurred during life, I have found the cardia so dilated that two or three fingers might be readily introduced into it.

It is perfectly possible for a horse to vomit and recover (showing that it had not a ruptured stomach), and it is not unusual to have attempts at or actual vomition when the small intestines are twisted.

The only case of vomiting I have seen in the horse which resembled the distressing appearance presented by the human subject was in a case of volvulus of the small bowels; the ingesta gushed in a stream from both nostrils, the horse lying on his chest with the nose extended; moreover, it was the only case I have observed where any sound accompanied the expiratory effort.

Vomiting in the horse is not as a rule attended by any distressing symptoms; the ingesta dribbles away from one or both nostrils; occasionally an effort may be made on the part of the patient, the head being depressed to facilitate expulsion. More than this is very rarely seen.

Why a horse should vomit more often with a ruptured stomach than a sound one is a fact I cannot explain.

It is important to notice in connection with the subject of vomiting, that agents such as tartar emetic which excite vomiting by their action on the cerebral centre, have no effect on the horse, nor do horses vomit as the result of sea-sickness, though they suffer extremely from it. The same remarks apply to ruminants.

In those animals where vomiting is a natural process, the three important operations are the dilatation of the cardia by active contraction of the longitudinal fibres of the œsophagus, pressure on the walls of the stomach by the abdominal muscles, and closure of the pylorus.

Rumination.

The physiology of rumination has been principally worked out in France by Flourens and Colin, and our knowledge of this singular process is based entirely on their observations.

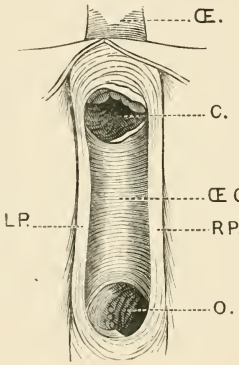


Fig. 10.—Diagram of the Œsophageal Groove.

Œ, œsophagus entering the stomach ; C, its cardiac opening ; RP, right pillar of œsophageal groove ; LP, left pillar of the same ; O, opening into the omasum ; ŒG, œsophageal groove extending from C to O. To the right of the figure is the rumen, to the left the reticulum. (After Carpenter.)

The œsophagus in ruminants enters the rumen and forms a singular groove or channel known as the œsophageal, which on the left communicates with the first and second stomachs, and on the right, by a very small opening, with the third stomach (Fig. 10). In this way food coming down the œsophagus may enter either of the three first

stomachs, the choice of stomach being determined, as we shall presently point out, by the condition in which the food is swallowed.

The œsophageal groove possesses two so-called lips or pillars, the anterior being formed by the reticulum, the posterior by the rumen. These pillars are composed of involuntary muscular fibres arranged longitudinally and transversely, by which means the groove can be shortened and constricted. By a contraction of the pillars the third stomach may be shut off from the first and second, and the opening into it brought nearly into apposition with the œsophagus; when the pillars are relaxed the œsophagus communicates more directly with the first and second stomachs. Another function of the groove is to cut off a pellet of food pressed into it by the contraction of the rumen and reticulum, the pellet or bolus being then passed into the œsophagus for remastication.

The food which has been lightly crushed in the mouth enters the rumen, meeting there with material from the last meal, as the rumen never empties itself. Here the maceration previously spoken of occurs, the food the whole time being slowly and deliberately churned. In the second stomach the same changes are occurring as in the rumen.

In rumination the œsophageal groove has been considered to play an important part; but Colin has shown that even if the lips be stitched together rumination may occur, so that the theory that the bolus is formed between the lips of the canal, and forced up the œsophagus by the powerful contraction of the rumen, is not correct according to this observer. What he says occurs is, that during the churning movement the food is gently pressed against the lips of the groove, when, by a spasmodic contraction of the diaphragm and abdominal muscles, some of the liquid from the reticulum and some of the solid from the rumen is carried up the œsophagus, which latter by the contraction of its funnel-shaped extremity cuts off the bolus, and by its reversed peristaltic action conveys it to the mouth. In passing under the velum palati the liquid portion is

squeezed out and is at once reswallowed, and passes to the third stomach, whilst the solid mass undergoes grinding. After the bolus is reswallowed, it may either pass again to the rumen, or, if in a finely comminuted condition, it passes at once from the œsophagus into the third stomach.

Flourens excised the reticulum, but this did not interfere with the process of rumination.

Rumination can only be performed by means of the united action of the walls of the stomach, abdominal walls, and diaphragm; it is impossible when the abdominal muscles or the walls of the stomach are paralysed; it can occur if the diaphragm be paralysed, but only through an extra effort of the abdominal muscles. The pillars of the diaphragm of the ox are specially arranged, so as to prevent compression of the œsophagus when the diaphragm contracts (Steel).* Further, rumination is only possible when the stomach contains a fair amount of food and a considerable quantity of liquid.

The ascent of the food in the œsophagus can be distinctly seen in the neck, and a sound may be heard on auscultation over the region of the œsophagus, due to the passage of the bolus with its fluid admixture. The amount of each bolus has been estimated by Colin at 3½ ozs. to 4 ozs. Its formation in the stomach and ascent will occupy about three seconds, and its descent after remastication one and a half seconds; its remastication occupies about fifty seconds. Altogether, Colin has calculated that a period of at least seven hours is required for the process of rumination.

During rumination the parotids secrete, but not the submaxillary or sublingual glands.

Rumination is a reflex nervous act, the centre of which is probably in the medulla. The nerves in the rumen convey the sensation to the brain by means of the pneumogastrics, which if divided cause rumination to be suspended.

The Nervous Mechanism of the Stomach.—Of this we know

* 'Diseases of the Ox,' J. H. Steel.

very little; as previously mentioned, we have no knowledge of the nerves which govern the secretion of gastric juice; there is no nerve the artificial stimulation of which has led to a secretion of the fluid.

The movements of the wall of the stomach are excited by the presence of food or irritation applied to the mucous membrane, and these movements may be increased by stimulation of the vagus nerve. It is found, however, that when the nerves leading to the stomach are divided so as to completely cut the organ off from any nervous influence, it still possesses the power of contraction, this being probably induced by the ganglia found in its walls.

The stomach is supplied by the pneumogastrics, which are here both non-medullated nerves, and also by the splanchnics through the semilunar ganglion. Irritation of the vagus leads to powerful contraction of the stomach walls, whilst irritation of the splanchnics causes the movement to cease; the vagus is therefore an augmentor nerve to the muscle of the stomach, whilst the splanchnics are inhibitory. On the contrary, the vagus supplies the blood-vessels of the stomach with inhibitory fibres, whilst the splanchnics supply them with constrictor fibres.

It is probable that the different muscular layers forming the wall of the stomach have a separate source of nerve supply, so that the circular can act independently of the longitudinal fibres.

Of the fibres opening and closing the cardia and pylorus we have no knowledge.

It has been previously mentioned that the nerve supply to the third stomach of the ox is quite distinct from that of the other stomachs; irritation of the pneumogastric produces contraction of all the stomachs but the omasum.

Intestinal Digestion.

Small Intestines.—The chyme which is poured from the stomach into the small intestines meets here with three other digestive fluids, viz., the succus entericus, the bile, and the pancreatic juice.

The **Succus Entericus** is prepared by the glands of the small intestines. In the duodenum we meet with the glands of Brunner and the follicles of Lieberkühn, the latter supplying a considerable quantity of intestinal juice, whilst the secretion from the former is scanty. Brunner's glands, which are very large in the horse, are arranged on the same principle as the gastric glands, whilst those of Lieberkühn are tubular glands, amongst the lining cylindrical epithelial cells of which numerous mucus-forming goblet cells may be found.

Colin endeavoured to obtain succus entericus by clamping a loop of bowel in the horse; by this means he obtained from 6½ feet of small intestine 2·8 ozs. to 4 ozs. of fluid in half an hour.

We have no satisfactory analysis of intestinal fluid in the horse; it is probable that the methods adopted to obtain it are not completely satisfactory, nor is it likely that, in spite of the precautions taken, it can be obtained free from bile, pancreatic fluid, or gastric juice. Colin states that the juice he obtained was mixed with a little mucus, which he got rid of by filtration; the fluid was then clear, of slightly yellow colour, saltish taste, alkaline reaction, specific gravity 1010, and its analysis showed it to be composed as follows:

Water - - - -	98·15
Albumin - - - -	·45
Chloride of sodium Chloride of potassium Phosphate and carbonate of soda	1·45

Colin endeavoured to obtain the secretion of Brunner's glands in the horse by ligaturing the common duct and pylorus, and emptying the bowel. In an hour he obtained 2·8 ozs. of viscous thick liquid of saline taste, slightly alkaline reaction, specific gravity 1008, and it was found to give the following analysis:

Water - - - -	98·47
Mucus - - - -	·95
Chloride of sodium Carbonate of soda - -	·48
Hypophosphate of lime - -	·10

This fluid did not coagulate on heating, nor did it form an emulsion with fatty matter.

According to Ellenberger and Hofmeister, the succus entericus contains three ferments. Starch can be converted into sugar, cane-sugar into grape-sugar (being the only body secretion, so far as we are aware, which possesses this power), and proteids are converted into peptones. These results were also previously obtained by Colin. They do not harmonize with the views of human physiologists, who attribute but a slight action to the intestinal fluid, and consider its chief function is to change maltose into dextrose. Bunge considers that in the human subject the chief use of the intestinal fluid is to neutralize the acid of the intestinal contents, which it is capable of doing owing to the considerable quantity of carbonate of soda it contains; its further function is to emulsify fats with the surplus soda.

This view will not hold good for the horse, as the contents of the stomach are no doubt neutralized by the pancreatic and biliary secretions immediately or shortly after they leave the stomach, so much so that on the duodenal side of the pylorus the reaction of previously acid chyme is neutral, and a few inches further back alkaline; this alkaline reaction, faint at first, becomes more marked as we reach the ileum.

Reaction of the Contents.—It is strange that on questions of fact any difference of opinion should exist. Ellenberger describes the small intestines as two-thirds acid, then neutral as far as the ileum, where it becomes alkaline. I have only once found it otherwise than alkaline throughout. He further states that in the fasting horse the contents are alkaline, but that in the digesting animal, whether horse, ox, or sheep, they are acid, the acidity decreasing after passing the common duct, and becoming decidedly alkaline at the lower, or what we would call the posterior, portion of the small intestine. This, as I have said, does not agree with my experience in the horse. It is usual to find the duodenum neutral. As we approach the middle of the small intestines the reaction becomes faintly alkaline, whilst

in the ileum the contents are always markedly alkaline. I have only once found them acid in the horse, no matter what diet has been given, or the period of digestion; neutral or faintly alkaline in the anterior part of its course, markedly alkaline in the posterior portion, is doubtless the rule rather than the exception.

Physical Characters of the Chyme.—The chyme having passed into the bowel, its appearance at once changes, for the acid albumin is precipitated by the alkaline secretion found there. It is now observed that the material consists of clots floating or suspended in a yellowish fluid, extremely slimy in nature, and resembling in appearance, through its precipitated albumin, nasal mucus suspended in fluid. The proportion of mucin must be considerable, judging from the manner in which it pours, and this mucus is probably derived from the stomach. Throughout the small intestines this condition obtains, viz., a yellow, frothy, precipitated, slimy, intestinal fluid; but we observe in that fluid taken from the latter part of the small intestines that it has a distinctly faecal odour, while that from the early intestines has a peculiar mawkish smell. In the ileum the proportion of fluid material is reduced considerably in amount, and we are capable of recognising the nature of the ingesta, which previously was almost impossible.

As the flow of material into the small intestines is controlled by a sphincter, so is the flow out of it. The ileum is a remarkably thick and powerful bowel; it is always found contracted and containing ingesta, which is dry compared with that found in the anterior portion of the bowel. One of the functions of the ileum is to control the passage of material into the caecum.

Colin describes the food as circulating between the pylorus and ileum, viz., that it is poured backwards and forwards in order to expose it sufficiently to the absorbent surface. This would necessitate a reversed peristaltic action. He says that were it not for this the material could not be acted upon and absorbed, as the passage of fluid through the small intestines is so very rapid. It

would never have occurred to me that the fluid material of the small intestines passed to and fro between the stomach and the ileum, exposed twenty times over, as Colin expresses it, to the absorbent surface of the bowels. He must have observed this as the result of his vivisections.

Experiment shows that water will pass from the stomach to the cæcum in from five to fifteen minutes. By applying the ear over the duodenum as it passes under the last rib on the right side, I have heard the water which a horse at that moment was drinking rushing through the intestines on its way to the cæcum.

One is always struck by the fact that the small intestines are never seen full, in fact, are often practically empty. From this I judge that material passes very rapidly through them. This material is always in a liquid condition excepting at the ileum; the fluid is derived from the secretions poured into and originating in the bowel, and that active absorption goes on in the intestines is proved by the difference in the physical characters of the contents, say in the middle of the small intestines and at their termination.

The rate at which the chyme passes through the small intestines will vary with the nature of the food, and the frequency with which the horse is fed. Ellenberger says it reaches the cæcum six hours after feeding, but has not entirely passed into this bowel for twelve or even twenty hours. I have known it reach the cæcum in four hours.

The remaining digestive fluids which the chyme meets with in the small intestines are the bile and pancreatic juice; the action of these on food is described in the chapter dealing with the liver and pancreas. The little we know about the absorption of lymph and chyle, and their elaboration before reaching the blood, are points which must be reserved for the chapter on 'Absorption.'

Large Intestines.—There can be no doubt that in solipeds digestion in the large intestines is a very important process; at least, we judge so from the fact of their enormous development. In many respects they present a considerable contrast to the small intestines; for instance, they are

always found filled with ingesta, the contents are more solid, the material lies a considerable time in them, and there are no juices other than the succus entericus poured into the bowel. These are points exactly opposed to what we have found in the small intestines.

The bowels which we speak of as the large intestines are the cæcum, double and single colon, and the rectum.

The **Cæcum** has been described by Ellenberger as a second stomach; its enormous capacity, fantastic shape, etc., have always rendered it an intestine of considerable interest. To my mind its most remarkable feature is that it is a bag, the opening into and out of which are both found at the upper part, close together, the exit, strange to say, being above the entrance, so that the contents have to work against gravity in order to obtain an entry into the next intestine, the double colon. The contents of the cæcum are always fluid, sometimes quite watery, occasionally of the colour and consistence of pea-soup, in which condition they are full of gas bubbles. When watery the fluid is generally brown in colour, with particles of ingesta floating about in it. The reaction of the contents is always alkaline; Colin, Ellenberger, and I all agree on this point.*

My own view of the function of the cæcum is that it is certainly not a second stomach so far as food is concerned; it is, however, most admirably arranged as a receptacle for fluids, and though undoubtedly absorption occurs from it, and digestion of cellulose occurs in it, yet I believe its chief function is the storing up of water for the wants of the body and the digestive requirements, for it is absolutely certain that digestion in the horse can only be properly carried out when the contents are kept in a fairly fluid condition. I do not say that the cæcum produces no digestive changes in the food, especially in the face of Ellenberger's and Hofmeister's experiments, who hold that the digestion in the cæcum is an important one, but I consider its digestive functions subordinate to its water-holding one.

Ellenberger views the cæcum as a bowel for the digestion

* I once found the cæcum acid.

of cellulose, where by churning, maceration, and decomposition, this substance is dissolved and rendered fit for absorption, and he likens it to the stomach of ruminants and the crop of birds; he further considers the cæcum exists owing to the small size of the stomach and the rapidity with which the contents are sent along the small intestines. It has also a large secreting surface, the glands being like those of Lieberkühn, and he considers that absorption takes place from the cæcum.

This observer's experiments demonstrated that the entire 'feed' reached this bowel between 12 and 24 hours after entering the stomach, that it remained 24 hours in the cæcum, and that during this time 10 to 30 per cent. of the cellulose disappeared. The digestion of cellulose is no doubt a very important matter, especially as we know that the poorer the food the more cellulose is digested; but I am not prepared to admit that food remains in the cæcum 24 hours, and I believe that cellulose digestion principally, though not entirely, occurs in the colon. The gas found in the cæcum chiefly arises from the decomposition of cellulose.

My experiments on digestion have shown that ingesta may be in the cæcum 3 to 4 hours after entering the mouth, and I am quite clear on the point that oats may reach even some distance along the colon in 4 hours from the time of feeding, though I regard this as exceptionally rapid.

I fed a horse, which had never had maize in its life, and had not tasted oats for two or three years, with, first, $2\frac{1}{2}$ lbs. of maize, and 17 hours later with 4 lbs. of oats. He was destroyed 4 hours from the time of commencing to eat the oats. Much maize and a few oats were found in the pelvic flexure of the colon, and a certain proportion of maize and a quantity of oats in the stomach. This bears out what we have said about gastric digestion slowing off (p. 115), and proves how great is the distance food may travel through the bowels in a short time, though I consider in this case its progress was much more rapid than usual.

Colin believes that in the cæcum starch can be converted into sugar, fats emulsified, and that active absorption of assimilable matters occurs.

It is remarkable how the material finds its way against gravity out of the cæcum. The capacious folds in the intestine are likened by Colin to the buckets of the Persian water-wheel, by which means the fluid is handed up and passed on into the colon.

In the absence of experimental evidence, I would hardly like to suggest that food may pass directly from the opening of the ileum into the colon, but I certainly have reason for thinking that this may occur.

The Colon.—The direction taken by the colon of the horse is remarkable. It commences high under the spine on the right side, its origin being very narrow, but it immediately becomes of immense size. It descends towards the sternum, and, curving to the left side, rests on the ensiform cartilage and inferior abdominal wall. The colon now ascends towards the pelvis, and here makes a curve, the bowel becoming very narrow in calibre. The pelvic flexure having been formed, the bowel retraces its steps towards where it started from; running on top of the previously described portion it descends towards the diaphragm, gradually getting larger in calibre, and then ascends towards the loin, being here of immense volume—in fact, at its largest diameter; it then suddenly contracts, and forms the single colon. The object of the difference in the volume of the double colon appears to be for the convenience of its accommodation in the abdominal cavity. The double colon may be divided into four portions for convenience of description: the ingesta in the first and third descend, in the second and fourth they ascend. We find that the physical characters of the contents are not the same throughout. In the first colon the food is fairly firm, and the particles of corn, etc., can be readily recognised. In the second colon the material is becoming more fluid, whilst at the pelvic flexure the contents are invariably in a liquid pea-soup condition, and the particles composing

them are not readily recognised. In the third colon the material becomes firmer, but only slightly so, and bubbles of gas are being constantly given off from its surface. In the fourth colon the entire ingesta are like thick soup, the surface covered with gas bubbles, and the material composing them is in a finely comminuted condition; for the first foot or so of the single colon this condition is maintained, when quite suddenly the contents are found solid and formed into balls. The remarkable suddenness of this change is invariable in a state of health, and indicates the most active absorption, perhaps the most active absorption of fluid in the intestinal canal.

The entire contents of the colon are yellow in colour or yellowish green, rapidly becoming brown or olive-green on exposure to light, or, what is more probable, to the oxygen of the air. The contents of the colon are normally alkaline throughout. I once, however, found them acid.

The muscular movements of the large intestine are much slower than those of the small bowels, for the food has to remain a longer time in contact with the absorbing surface; at least forty-eight hours.

In the colon the food undergoes a further elaboration. Thanhoffer has claimed that starch may be converted into sugar, and proteids into peptones, and I see no reason why the latter, at any rate, should not take place, for it is positively certain that in the colon much material may be found which requires further acting upon; this we may see in almost any feeding experiment, particularly with grain. Cellulose, no doubt, is here also acted upon; perhaps the chief action of the colon is directed against the cellulose.

In my opinion it is impossible that this enormous intestine can exist simply as a reservoir for ingesta, as has been suggested. Such a view is incompatible with its structure or the appearance of its contents.

The marked fermentative changes occurring in the fourth portion of the colon are probably especially associated with cellulose digestion, as we know that the intestinal gases consist amongst others of CH_4.

Unless cellulose performs some more important function than that of yielding sugar, it is difficult to conceive that such enormous and elaborate bowels should exist for its digestion. We are even ignorant of the means whereby it undergoes digestion. A cellulose ferment, such as that found by Brown in oats and barley (p. 129), is probably the explanation, but such has not yet been found in hay, or the digestion may occur under the influence of intestinal organisms. Bunge imagines that the epithelial cells of the intestine dissolve cellulose as well as convert dextrin into sugar.

We have previously (p. 16) mentioned Bunge's views on the value of cellulose in a diet. He considers that it is absolutely essential to animals with a long intestine, as it acts as a natural stimulus to the bowel, and promotes peristalsis.

In the single colon we have noted the remarkable and sudden change of highly fluid, thick, soup-like ingesta, into comparatively dry fæces. As the material moves towards the anus it becomes drier and drier, and more thoroughly formed into balls by the action of the bowel-sacs, which squeeze the mass into a round or oval shape. The contents of this portion are still alkaline, or slightly so, though as we approach the rectum a distinctly acid reaction is obtained on the surface of the fæces, though at this time the interior of the ball may be, and often is, alkaline; the converse of this may also be obtained. In the rectum the single balls collect in masses, to be forced out of the body at the next evacuation. The reaction of this mass is acid, the colour depending on the food, but having rather a reddish-yellow or brownish tint on ordinary diet.

Absorption from the single colon and rectum is very rapid. Animals may be killed by the rectal injection of strychnine, or life may be supported by nutritive enemata. Narcosis can also be produced by the rectal administration of ether.

Putrefactive Processes in the Intestinal Canal.—We may here consider the nature of the putrefactive processes

occurring in the digestive canal, the presence of which we recognise by the production of ill-smelling gases.

In the anterior part of the small intestine no putrefactive odour is obtained, but after the admixture and action of the pancreatic juice a distinctly fæcal odour is given to the contents. There can be no doubt of the large number of organisms found in the small intestine, which, to a certain extent, may be useful in assisting digestion, especially that of proteids, and perhaps of fats. By means of organisms also leucin and tyrosin, indol and skatol, lactic and butyric acids, may be formed (Halliburton), and the function of these organisms may further—according to the same observer—be protective in destroying poisonous products, such as cholin (the alkaloid derived from lecithin).

The decomposition of proteids in the large intestine leads to the formation of carbonic acid, sulphuretted hydrogen, ammonia, phenol, kresol, skatol, and certain organic sulphur compounds; the latter, with phenol and indican, are excreted by the kidneys, and in carnivora and omnivora are regarded as a measure of the putrefactive processes occurring in the bowel. This, however, will not hold good for the herbivora, as the phenol with them is largely derived from the food.

Phenol, or carbolic acid, is largely formed in the horse, and is excreted by the kidneys. Indol and skatol give to fæces their characteristic odour.

The longer the food remains in the bowel, the more indol and phenol is formed; they are decomposition processes, and have nothing to do with nutrition, and are got rid of in flesh-feeders by disinfecting the intestinal canal with calomel.

According to Tappeiner, phenol is found in the stomachs and intestines of cattle, skatol in the paunch, and indol in the large and small intestines. In the horse, indol is present up to the cæcum; in the colon, its place is taken by skatol. Phenol and ortho-kresol are found throughout the large intestines.

The fermentation in the intestines of the horse may be

either acid or alkaline, both leading to the production of marsh gas; but the acid fermentation occurs in the presence of skatol, whilst the alkaline occurs in the presence of indol (Ellenberger). Intestinal fermentation in the horse is allied to that occurring in the rumen of cattle. In all cases the fermentation can occur without the presence of oxygen.

By the decomposition of starchy matters lactic, formic, acetic, butyric, and propionic acids are formed. It is to some of these that the acid reaction of normal fæces is due.

In the large intestines of horses Colin describes no less than eight or ten species of Infusoria. The most characteristic of these are the Colopodes, recognisable by their ovoid form, with lateral indentation, at the base of which the mouth is found. Others have an ovoid form but lack the lateral indentation of the previous species; some have an elongated rectangular form, and others are unsymmetrical in shape. All these infusoria are found in the cæcum and anterior parts of the double colon; they die in the last part of the intestines, and leave nothing more than their débris in the excreta. In ruminants similar organisms are found in the rumen. As to the action of these organisms we know nothing.

The largest amount of gas found in the intestinal canal is in the cæcum and colon. The small intestines do not naturally contain much, whatever is formed there being probably rapidly passed into the large bowels. In these intestines we know that marsh-gas commonly exists, forming, with CO_2, the bulk of the gases present in these parts. We are all practically aware of the conditions arising in horses in the large bowels, and in cattle in the rumen, as the result of the fermentation of food—particularly green grass—and the enormous size to which the animal may be distended. In both the gas may generally be ignited a short distance away from the cannula, which has been passed into the parts to give relief, the CH_4, or marsh-gas, igniting readily on meeting with the proper proportion of oxygen.

The gases of the large intestine in the horse contain, according to Planer, 50 per cent. of carburetted hydrogen, 42 per cent. of nitrogen, and 8 per cent. of carbonic acid.

Tappeiner, quoted by Ellenberger, gives the following analysis of intestinal gases in the horse:

Small Intestines (Hay Diet).

	Anterior portion.	*Posterior portion.*
Carbonic acid	72	15
Sulphuretted hydrogen and hydrogen	19	24
Nitrogen	37	59

Large Intestines (Hay Diet).

	Cæcum.	*Colon.*	*Rectum.*
Carbonic acid and sulphuretted hydrogen	85·0	55·5	29·0
Hydrogen	2·0	1·7	1·0
Marsh-gas	11·0	33·0	56·0
Nitrogen	·9	10·0	13·0

On Corn and Hay Diet.

	Small Intestines.	*Colon.*	*Rectum.*
Carbonic acid	11·0	75·00	45·0
Hydrogen	4·0	·38	3·0
Nitrogen	84·0	6·00	12·0
Oxygen	·7	—	—
Marsh-gas	—	17·00	40·0

The Fæces.

The fæces consist of that portion of the food which is indigestible, together with that part which though digestible has escaped absorption. Mixed with these we have water, colouring substances, mucin, and other organic matters, inorganic salts, bile pigment, volatile fatty acids, remains of digestive fluids, organisms, etc.

The composition of the fæces depends largely on the diet. The following table from Gamgee* can only give a general idea of their nature:

* 'Our Domestic Animals in Health and Disease,' p. 253.

Approximate Composition of the Fæces of the

	Horse.	*Cow.*	*Sheep.*	*Pig.*
Water - -	76·0	84·0	58·0	80·0
Organic matter -	21·0	13·6	36·0	17·0
Mineral „ -	3·0	2·4	6·0	3·0
	100·0	100·0	100·0	100·0

Considerable differences exist amongst animals in the consistence of the fæces; they are moderately firm in the horse, pultaceous in the ox, and very hard in the sheep. These differences depend upon the amount of fluid they contain. It is necessary to remember that the proportion of fluid in the fæces does not depend upon the water consumed, but rather on the character of the food, the activity of intestinal peristalsis, and the energy with which absorption is carried out in the digestive canal. Succulent food in horses produces a liquid or pultaceous motion; other foods, such as hay and chaff, have a constipating effect, the fæces being small and hard; excess of nitrogenous matter in the food produces extreme fœtor of the dejecta, and frequently diarrhœa; nervous excitement rapidly induces a free action of the bowels, accompanied by very liquid fæces; this latter is explained by the increased production of peristaltic action.

The colour of the fæces in the horse is yellowish or brownish-red; they rapidly become darker on exposure to the air. When the animal is grass-fed the fæces are green, and when fed wholly on corn they become very yellow and more like wet bran in appearance.

The fæces of the horse are moulded into balls in the single colon, an intestine where, as we have previously indicated, the most active absorption of fluid must occur, for the contents becomes almost suddenly converted from a liquid into a solid condition.

The fæces of the horse are always acid, the acidity probably depending upon the development of some acid from the carbo-hydrates of the food.

Fæces contain, amongst the indigestible portion of the ingesta, lignin, a proportion of cellulose, husks of grains,

the downy hair found on the kernel of oats, vegetable tubes and spirals, starch and fat granules, gums, resins, chlorophyl, etc.; unabsorbed proteid, carbo-hydrate and fatty material; products of digestive fermentation, such as lactic, malic, butyric, succinic, acetic, and formic acids; leucin, tyrosin, indol, skatol, and phenol; biliary matters and altered bile pigment, which latter gives the colour to the dejecta, and is known as stercobilin; and, lastly, mineral matter in varying proportions. The fæces always float in water.

Amongst the inorganic matter silica exists in largest amounts, then potassium and phosphoric acid, sodium, lime, magnesium, and sulphuric acid, forming a smaller but still important proportion.

The horse excretes but little phosphoric acid by the kidneys, but considerable quantities pass with the fæces in the form of ammonio-magnesium phosphate. This salt is derived principally from the oats and bran of the food, and through collecting in the colon and becoming mixed with organic substances, frequently forms itself into calculi. Other intestinal calculi are formed from lime deposits in the bowel, and collections of the fine hairs from the kernels of oats form the so-called oat-hair calculus.

The following table by Roger gives the mineral composition of the fæces in every 100 parts of the ash:*

	Horse.	*Ox.*	*Sheep.*
Sodium chloride	·03	·23	·14
Potassium	11·30	2·91	8·32
Sodium	1·98	·98	3·28
Lime	4·63	5·71	18·15
Magnesium	3·84	11·47	5·45
Oxide of iron	1·44	5·22	2·10
Phosphoric acid	10·22	8·47	9·10
Sulphuric acid	1·83	1·77	2·69
Silica	62·40	62·54	50·11
Oxide of magnesium	2·13	—	—

Roger observed that the ash of herbivorous fæces contained scarcely any alkaline carbonates.

* Quoted by Ellenberger.

The **amount of fæces produced** in 24 hours varies with the quantity and nature of the food given. I have observed that on a diet consisting of 12 lbs. of hay, 6 lbs. of oats, and 3 lbs. of bran, that the average amount of fæces passed by fifteen horses during an experiment lasting seven days, amounted to 29 lbs. 13 ozs. in 24 hours, the fæces being weighed in their natural condition, viz., containing 76 per cent. water; the dry material of this bulk of fæces is about 7¼ lbs. More fæces are passed during the night than during the day. In the above experiment, during the 12 hours (6 p.m. to 6 a.m.), the average amount of fæces per horse was 18 lbs. 3 ozs., whilst from 6 a.m. to 6 p.m. the amount was 11 lbs. 10 ozs. The largest amount of fæces I have known a horse produce was an average of 73·3 lbs. (weighed in their natural state) for the 24 hours; the diet consisted of 12 lbs. of oats, 3 lbs. of bran, and 28 lbs. of hay.

In an experiment carried out for several months with different horses all receiving 12 lbs. hay and varying proportions of bran and oats, the average daily amount of fæces, weighed in their natural state, amounted to 24 lbs.

A horse will evacuate the contents of the bowels about ten or twelve times in the 24 hours, and the food he consumes will take at least four days to pass through the body.

In the ox the amount of fæces in 24 hours is about 66 lbs. per diem, containing about 10 lbs. of dry material.

The **odour of fæces** is distinctly unpleasant, due to the presence of indol and skatol. In disease the fæces are often extremely fœtid; the odour probably depends upon the indol and skatol and the decomposing unabsorbed proteid.

The act of **defæcation** is performed by a contraction of the rectum, assisted by the abdominal muscles, the glottis being closed. In the horse the contraction of the rectum alone is sufficient to expel its contents; this is well shown by the fact that this animal can defæcate while trotting. The anal sphincter dilates under the pressure of the fæces, the tonic contraction of the muscle—the centre for which

exists in the lumbar cord—having been liberated by a voluntary act. If this centre be destroyed the anus becomes flaccid and the rectum remains full, showing that the mechanism which contracts the anus also contracts the rectum.

After the contents of the bowels have been evacuated the sphincter closes, and in doing so imprisons a portion of the mucus membrane of the bowel, which temporarily remains everted and is then gradually withdrawn.

Meconium is the dark-green material found in the intestines of the fœtus. It consists of biliary matters, both acids and pigments, fatty acids, and cholesterin; whilst the salts of magnesium and calcium, phosphoric and sulphuric acids, sodium chloride, soda, and potash are also found in it. The meconium is the product of liver excretion.

Nervous Mechanism of the Intestinal Canal.—What we have previously said about the stomach nervous mechanism applies equally to the bowels. Secretion can be excited by chemical, thermal, and other stimuli, the normal irritation being naturally the food passing along the canal. Irritation of the vagus produces no influence on the secretion; extirpation of the cœliac and mesenteric plexuses causes a profuse secretion; and in the same way division of the nerves leading to a loop of bowel produces an outpouring of intestinal fluid. The injection of pilocarpine causes a considerable secretion, and powerful contraction of the intestinal walls; the action of this drug on the horse, and its elective affinity for the salivary, pancreatic, and intestinal glands is very remarkable.

The intestines contain local ganglia, and these are capable of sustaining the movements of the bowel when all other sources of nerve-supply are cut off; this is well seen in the movements of the intestines of a recently-destroyed horse. The augmentor fibres from the vagus, and the inhibitory fibres from the sympathetic system, such as are described on p. 141, apply with equal force to the muscular wall of the intestinal canal; it is possible that the two intestinal muscles have a distinct source of

supply; in the same way the opposite action of the vagus and sympathetic on the bloodvessels of the stomach are observed to apply to the intestinal walls.

Practically we know that bulk is necessary for intestinal digestion, a horse cannot be kept in condition on concentrated food; bulk promotes intestinal peristalsis, and probably the presence of gases in the intestine within certain limits also has an influence in this direction.

When the blood-supply to the bowel is cut off, increased peristaltic action occurs; this is the probable explanation of the movements seen in bowels removed from an animal recently destroyed, and is possibly the cause of the expulsion of the contents of the rectum when life is suddenly and violently taken away.

The nervous mechanisms employed in defæcation are described on p. 156.

CHAPTER VIII.

THE LIVER AND PANCREAS.

Bile.

The bile is a fluid of an alkaline reaction, and of a yellowish-green or dark-green colour in herbivora, though in man and carnivora it is of a golden red tint. This difference in colour depends upon the character of the pigment present, to which we will shortly allude.

Bile has a bitter taste, a specific gravity in the ox of 1022 to 1025, in the sheep from 1025 to 1031, in the horse 1005. By standing in the gall-bladder the solids are considerably increased, owing to an absorption of part of the water of the bile. Bile taken direct from the liver is watery in consistence, that taken from the gall-bladder is viscid, due to admixture with mucin during its stay in the latter receptacle. The secretion contains no proteid, which is somewhat remarkable. It contains mucin (which is derived from the gall-bladder), biliary pigments, bile acids, fats, soaps, lecithin, cholesterin, a small quantity of diastatic ferment, and inorganic salts. The secretion in the horse contains no mucin, and, according to Ellenberger, there is very little mucin in the bile of sheep.

The dried alcoholic extract of bile contains in the ox 3·58 per cent. of sulphur, sheep 5·71 per cent., and pig ·33 per cent.* The gases found in bile are CO_2, and traces of O and N.

The chief inorganic salts are sodium chloride and sodium phosphate, besides which are found lime, magnesium,

* Quoted by Halliburton.

potassium, iron, phosphoric and sulphuric acids; the sodium salts are always the largest. The iron, which exists as phosphate, is probably derived from the hæmoglobin of the blood during the formation of the bile pigments.

The following analysis of ox-bile is given by Berzelius :*

Water	90·4
Solids	9·6
Bile salts	8·0, cholesterin 2·5 per cent.
Lecithin, cholesterin, fats, soaps	
Mucus and pigment	·3
Inorganic salts	1·3, including iron ·003 to ·006.†

The following table is compiled from Ellenberger :

	Ox Bile.	*Sheep Bile.*	*Horse Bile.*
Water	92·91	86·90	Water 95 per cent.
Bile acids	5·61	16·69	Solids 5 „ „
Bile pigments	·32	·29	
Fat	·03	(?)	
Mucus	·51	·94	
Salts	1·30	11·83	

Percentage Composition of the Ash of Ox Bile.

Sodium chloride	27·7	Manganese peroxide	·12
Potassium	4·8	Phosphoric acid	10·45
Sodium	37·7	Sulphuric „	6·39
Lime	1·4	Carbonic „	11·26
Magnesia	·53	Silica	·36
Iron oxide	·23		

It is to be regretted that no complete analysis has been made of bile in the horse, but the difficulties attending its collection in a pure state are obvious.

The fat present is in the form of lecithin, a complex nitrogenous substance united with phosphoric acid, and found in several of the tissues and secretions of the body.

Cholesterin, another singular substance, is an alcohol and not a fat, though from its appearance it has been termed bile-fat. It is found in very regular quantities, and forms

* Quoted by M'Kendrick.

† Young, quoted by Halliburton.

the principal constituent of certain gall-stones. It is kept in solution in the bile by means of the bile salts.

The **Bile Pigments** are two in number, bilirubin and biliverdin; the latter is produced by oxidation from the former. Bilirubin is the colouring matter of human bile and that of carnivora, whilst biliverdin gives the colour to that of herbivorous animals.

Both pigments are insoluble in water, but soluble in alkalies; in the bile they are held in solution by the bile acids and alkalies. Bilirubin may be obtained from gall-stones of the ox in the form of an orange-coloured powder, which can be made to crystallize in rhombic tablets and prisms. If an alkaline solution of bilirubin be exposed to the air it becomes biliverdin by oxidation, and this latter pigment by appropriate treatment may be obtained as a green powder.

Both colouring matters of the bile behave like acids, forming soluble compounds with metals of the potassium group, insoluble ones with those of the calcium group (Bunge).

On the addition of nitric acid (containing nitrous acid) to the bile pigments, a play of colours is observed, known as Gmelin's test. In the case of bilirubin the colours pass from yellowish red to green, then to blue, violet, red, and yellow. Each of these colours is indicative of a different degree of oxidation of the original bilirubin. Biliverdin gives the same play of colours excepting the initial yellowish red, which is, of course, absent.

Although bilirubin has not been obtained from hæmoglobin, there appears to be no reasonable doubt that this is the source of the pigment, for hæmoglobin may be readily decomposed, yielding a proteid and hæmatin, and if this hæmatin be deprived of iron, the residue thus obtained is not very dissimilar in composition to bilirubin. Old blood-clots contain an iron free substance known as hæmatoidin, which is identical in composition with bilirubin. The iron which is found in the bile probably results partly from the hæmoglobin after it has become converted into the iron free substance bilirubin.

The actual production of bile pigments takes place in the liver, but the means by which the latter organ is furnished with free hæmoglobin for the purpose is still obscure.

The **Bile Salts** are two in number, glycocholate and taurocholate of soda. They are formed by the union of cholalic acid with glycin or taurin, and exist in combination with soda. These salts are found to exist in varying proportions in different animals—thus, while glycocholate of soda is largely found in herbivora, taurocholate is the principal constituent of dog's bile, and in pig's bile hyoglycocholic and hyotaurocholic acids are found. Both salts are soluble in water, have a decided alkaline reaction, rotate the plane of polarized light to the right, and may be obtained in the crystalline form of acicular needles highly deliquescent.

Glycocholic acid is the chief bile acid in herbivora; it is produced by the union of glycin with cholalic acid. Glycocholic acid is diminished by an animal diet, and increased by a vegetable one.

Taurocholic acid is produced from taurin and cholalic acid, and exists principally in carnivora, though small quantities may be found in the ox. This acid differs from the first characteristically by containing sulphur, by which it shows its proteid origin.

In the intestine the constituents of the bile are absorbed: both acids are decomposed or split up by ferments into cholalic acid and glycin or taurin, the two latter being reabsorbed.

Glycin or glycocoll originates from proteids, and if administered it reappears externally as urea. It cannot be traced in the free state in the body, but occurs with benzoic acid, from which combination is formed hippuric acid (Bunge).

In Pettenkofer's test for bile acids the reaction obtained is due to cholalic acid. The test is performed as follows: A drop of the fluid is placed on a white earthenware surface, and to it is added a drop of a strong solution of cane-sugar, and a similar quantity of strong sulphuric acid; a beautiful purple-red colour forms, which may be assisted

by warming. This test is not solely indicative of bile acids; other substances also give it.

The origin of the bile acids is wrapped in obscurity: taurin is formed in the body, probably also glycin, and cholalic acid is formed in the liver. Beyond this we know but little, not even why glycin should predominate in some animals and taurin in others.

Bile is secreted under a very low pressure, which is the reverse of what occurs in the saliva; but low as the pressure is (·58 inch of mercury), it is higher than that of the blood in the portal vein—in fact double. The secretion of bile is a continuous one; whether the horse be in full digestion or fasting the flow does not intermit like the saliva. During digestion the amount of bile increases.

Quantity of Bile.—The amount secreted varies, but is greater in herbivora than carnivora. Colin's experiments gave him the following amounts as hourly secretions:

Ox	-	-	$3\frac{1}{2}$ ozs. to $4\frac{1}{4}$ ozs. per hour.
Sheep	-	-	$\frac{1}{4}$ oz. to $5\frac{1}{2}$ ozs. „ „
Horse	-	-	$8\frac{3}{4}$ ozs. to $10\frac{1}{2}$ ozs. „ „

In those animals possessing a gall-bladder this receptacle is filled during abstinence, or, if it be empty, it is filled even during digestion. It empties itself through its own contractions.

The nervous influence controlling the secretion of bile is unknown.

The **Use of the Bile** from a digestive point of view is very disappointing, inasmuch as it does not digest in the sense that pepsin and trypsin do. That it is intimately connected with that of the pancreas would appear to be the case, from the fact that the secretions are poured out either close together in the bowel, or, as in the horse, by a duct common to the two glands. As the horse possesses no gall-bladder, the secretion as fast as it is prepared is poured into the intestine; not so with the ox, where it is stored up in a capacious gall-bladder until required. From what has been previously said, we can see the reason of this remark-

able difference in two purely vegetable-feeding animals. In the horse food in greater or less quantity is always passing along the small bowels; as the stomach under ordinary circumstances practically never empties itself, it is, therefore, necessary that bile should always be poured into the intestine In the ox, where the food makes a prolonged stay in the stomachs, bile is only required at the moment when the chyme finds its way into the duodenum: in the interval it is stored up ready for use.

The bile being alkaline, its first action on the chyme is to precipitate the acid albumin which has escaped the process of peptonizing in the stomach. One effect of this is probably to protect the pancreatic ferments from the pepsin of the gastric juice, and further, to delay the progress of the chyme along the bowel, and so give the pancreatic juice time to act. On proteids the bile has no digestive action; on fats, however, it has a solvent and emulsifying effect, being more active in the presence than in the absence of pancreatic juice. Bile cannot split up fats into fatty acids and glycerine as the pancreas does, but if free fatty acids are present the bile salts are decomposed, their soda set free, and soluble soaps formed; the soaps so formed assist in rendering the emulsifying effect of the bile permanent and the absorption of fat much easier. Fat will not readily pass through a membrane, but if the latter be first moistened with bile the passage is readily effected. On the starch of the food bile in the herbivora is said to exert some action, but it would appear that in this respect it mainly assists the pancreas, the juice of the latter being more active on starch in the presence of than in the absence of bile.

The further action of bile on the intestinal contents is to keep them from putrefaction and promote peristalsis, for it is found that when the bile is prevented from entering the intestines, constipation and extreme fetor of the intestinal contents results.

Bunge states that the clay-coloured faeces obtained in jaundice is due to the presence of unacted-on fat; the fat

encloses the proteids, which putrefy, hence the odour. The bile, he states, is not an antiseptic, but acts as a natural purgative and keeps up intestinal peristalsis, and by so doing hurries the food out of the system before it undergoes putrid decomposition.

Some of the constituents of the bile are broken up in the bowel; for instance, the bile acids yield cholalic acid, setting free glycin and taurin. The latter, being absorbed again are carried to the liver, and may probably there excite the further secretion of bile acids; cholalic acid is excreted with the fæces. In the bowels the pigments also undergo change, yielding stercobilin (the colouring matter of the fæces) and urobilin (the colouring substance of the urine).

Glycogen.

It is quite certain that the largest gland in the body must have some other function than that of the secretion of a fluid of comparatively unimportant digestive power, and such is the case. The liver manufactures and stores up in its cells a peculiar substance known as **Glycogen**, or animal starch.

The literature of glycogen is extensive; perhaps no substance has given rise to greater controversy. All we can attempt here is to give a general and brief outline of a complicated subject on which much diversity of opinion has existed.

The sugar in the food, or that derived from starch-conversion, finds its way by means of the intestinal blood-vessels into the portal vein; from here it passes into the liver. Under ordinary circumstances it is stored up in the liver as glycogen, being, in fact, reconverted into a kind of animal starch, and it is gradually doled out to the system as sugar as the body is in need of it.

The liver regulates the amount of sugar which should pass into the blood; so much and no more is admitted to the circulating fluid, the amount varying between ·05 and ·15 per cent. The sugar in the blood of the ox was estimated by C. Bernard at ·17 per cent.; in the calf, ·1 per

cent.; and in the horse, ·09 per cent. (M'Kendrick). One use of the liver is to regulate this amount and avoid a surplus. During starvation the amount of glycogen in the liver falls, and eventually disappears; the liver has now liberated to the blood the entire amount of sugar it is capable of yielding. If food, particularly carbo-hydrates, be now taken, the store of glycogen is replenished, and the sugar-liberating function once more occurs.

The method by which the glycogen becomes converted in the liver into glucose (not maltose, as in the bowel), before being issued to the blood, is generally considered to be by means of a ferment (see p. 167), and this glucose, of course, reaches the general circulation through the hepatic veins.

It is curious to observe that the starch must first be converted into sugar before the bloodvessels of the bowel can take it up, then in the liver once more converted into a kind of starch, and, lastly, again into sugar before entering the blood.

Glycogen differs in some respects from starch, one of its principal differences being that it dissolves in cold water, and is stained reddish brown by iodine.

The total amount of glycogen obtained from a given quantity of food is not wholly stored in the liver, as the latter organ cannot contain more than about 10 per cent. of this substance, which would represent only a small amount of the soluble carbo-hydrates passing into the blood. We know as a fact that the liver, having taken up all the sugar it can from the portal vessels and converted it into stored-up glycogen, allows the balance to pass through the hepatic veins into the general circulation as sugar, and that it is deposited in other organs (principally the muscles) as glycogen for future use. The muscles of the horse contain in this way a considerable quantity of glycogen. Even after nine days' starvation, from 1 per cent. to 2·4 per cent. of glycogen was found by Aldehoff.* Blood contains no glycogen.

* Quoted by Bunge.

The use of glycogen is to supply muscular energy and animal heat. During work it diminishes in the muscles, and during rest it is stored up.

Foster warns us against regarding the glycogen of muscle as of any value in the production of muscular energy until it has actually become muscle. As he expresses it, 'It cannot be fired off as raw glycogen, or even as dextrose, in the interstices of the muscular fibre'; it must first become muscle.

The source of glycogen is a disputed point: carbo-hydrates, no doubt, contribute largely to its production; but there is reason to believe that proteids also assist in its formation. The majority of observers agree that fat takes no part in the production of glycogen.

The hepatic blood contains, roughly, twice as much sugar as the portal (Seegen, quoted by Halliburton). Lehmann states that in starving horses he found no sugar in the portal vein, although it was always to be detected in the hepatic vein.

When the liver is removed from the body the glycogen diminishes and the sugar increases. No ferment theory, according to Halliburton, is required to explain this conversion, as a diastatic ferment can be obtained from all living proteids. By the administration of glycerin the post-mortem conversion of glycogen into sugar may be prevented (Ransom).* The same observer discovered that the administration of glycerin also prevented the diabetes of rabbits which follows an injury of the medulla, and he concludes that glycerin inhibits the formation of sugar in the liver-cells.

If glycocin be injected into the blood, according to some observers the formation of glycogen in the liver as well as of urea is increased.

Bernard discovered that by puncturing the floor of the fourth ventricle sugar appeared in the urine. The explanation of this may be that it is due to paralysis of the blood-vessels of the liver, the nerves of which originate in the

* Quoted by Halliburton.

medulla; through paralysis the liver becomes gorged with blood, which is followed by sugar in the urine. This view appears to be the correct one, since stimulation of the upper end of the divided pneumogastric is followed by sugar in the urine, and this sugar is also produced by vaso-motor paralysis, the pneumogastric being a controlling nerve of the vaso-motor centre.

Further Uses of the Liver.

We have studied two uses of the liver, viz., the formation of bile and the storing up of glycogen; but we have yet other uses of this gland to detail.

The material carried by the portal vein to the liver contains, besides peptones, some other ultimate products of proteid digestion, viz., leucin and tyrosin; these are conveyed to the liver, and the leucin contributes to the formation of urea.

Carbonate of ammonia is converted in the body into urea and uric acid, and this change occurs in the liver. Possibly many of the antecedents of urea in the body are in the liver converted into this substance. This is a point to be dealt with more fully in the chapter on the urine—all we wish to impress here is the function the liver possesses of converting into urea and uric acid certain nitrogenous products of digestion.

As the result of proteid decomposition in the intestinal canal, certain aromatic compounds are formed: these are united with sulphuric acid, and got rid of by the kidneys as conjugated sulphuric acids. In this combination the previously poisonous proteid products are converted into non-poisonous ones, and this change is effected in the liver (Bunge.)

Here we have a very important function of the liver demonstrated, viz., as a neutralizer of poisons introduced into the blood by the intestines. Many metallic poisons are also arrested in the liver, notably mercury and arsenic.

The numerous and complicated changes produced by the liver may thus be summarized: It forms bile, regulates the

supply of sugar to the system, storing up as glycogen what is not required; it guards the systemic circulation against the introduction of certain nitrogenous poisons, such as ammonia, by converting them into urea and uric acid, and against other poisons of proteid origin by converting them into harmless products, by conjugation with alkaline sulphates (Bunge).

Pancreas.

The fluid secreted by the pancreas performs certain important functions in digestion. It is remarked by Bunge that there is scarcely any animal which does not possess a secretion allied to the pancreas; even those invertebrates without a peptic or biliary apparatus are in possession of one.

From the resemblance of the pancreas to the salivary glands, it has been termed the abdominal salivary gland. The pancreatic fluid from the herbivora can only be obtained with extreme difficulty; to establish a pancreatic fistula in the horse is a formidable operation, necessitating an incision from the sternum to the pubis and the turning back of the bowels. Colin has established these fistulæ both in the horse and ox; but the profound impression on the nervous system produced by such extensive interference, must considerably affect the character of the secretion and the amount manufactured.

Pancreatic fluid is alkaline, clear, colourless like water, and though viscid in some animals is not so in the horse. It has a saltish unpleasant taste, and a specific gravity of about 1010; the viscid secretion of the dog has a specific gravity of 1030.

The following analysis of the fluid in the horse is given by Hoppe-Seyler:*

Water -	-	982·53
Solids -	-	17·47
Organic matter		8·88 containing 8·6 of ferments.
Salts -	-	8·59 „ much sodium phosphate.

* Quoted by Halliburton.

The salts present are sodium chloride in abundance, potassium chloride in traces, sodium carbonate and phosphate, calcium and magnesium phosphates in small quantities. The total solids appear to be subject to great variation, but the salts are constant. The organic solids are remarkable for the amount of proteid present in them.

Uses of the Secretion.—The pancreatic juice is poured into the bowel in the horse by a duct common to the pancreas and liver; in the ox the two ducts are separate, and open within an inch or two of each other. I have seen a similar arrangement in the horse. Pancreatic juice is essentially a digestive fluid, acting as it does on all the elements of food, viz., proteids, fats, and carbo-hydrates: all of these undergo certain changes—the proteids into peptones, the fats into fatty acids and glycerin, and the carbo-hydrates into sugar. These changes are so definite that it has been assumed, with very good reason, that each is brought about by a distinctive ferment, though every attempt to isolate them has failed. It is convenient, however, to speak of them as separate ferments, the total amount of which in the horse has been estimated by Hoppe-Seyler to be 8·6 per 1000—forming, in fact, nearly the total organic matter existing in the secretion.

The ferments found in the pancreatic fluid are:

Trypsin—which converts proteids into peptones.
Amylopsin—which converts starch into sugar.
Steapsin—which splits up fats into fatty acids and glycerin.

A milk-curdling ferment has been described; but in adult digestion there can be but little need for one.

The action of this ferment on proteids is much the same as we have previously studied in the gastric juice, proteids being converted into peptones, especially those difficult of this conversion in the stomach, and the hemi-peptones of the stomach are split up into leucin and tyrosin; but there are certain important differences which serve to distinguish between proteid digestion in the stomach and that in the intestines, thus:

1. Peptic digestion is an acid one; pancreatic is essentially an alkaline one.

2. If fibrin be digested by trypsin, during the action of the ferment the fibrin does not swell up as in peptic digestion. Further, the fibrin is eroded by the action of trypsin, rather than dissolved as in peptic digestion.

3. The outcome of pancreatic digestion is an alkali-albumin, and not an acid one, as in the stomach; and the proteids in the case of pancreatic digestion undergo a change not only into peptones, but a portion of them is further converted into leucin, tyrosin, and other substances. The production of indol, phenol, and skatol in pancreatic proteid digestion cannot be regarded as due to the pancreas, but to the presence of micro-organisms and consequent putrefaction.

By these reactions it is easy to distinguish between a peptic and pancreatic digestion; it is very remarkable that peptone products can be obtained through the action of two such apparently opposite secretions as gastric and pancreatic juice.

The action on starchy food is to convert it into sugar, and this it is capable of doing with extreme rapidity; 15½ grains of pancreatic juice can convert in half an hour 71 grains of starch into sugar; the form of sugar produced is maltose, with a little glucose; the fluid has no action on cane-sugar, but on starch it acts on the unboiled as well as on the boiled variety.

On fats the action is very marked: the fats are first converted into an emulsion, by which means the particles of oil are finely divided; in the next stage the fat itself is split up into its constituents, viz., fatty acids and glycerin, and the former in the presence of an alkali forms soaps. The alkaline salts of the pancreatic juice assist in this action.

The pancreatic juice of the horse emulsifies less completely than that of other animals.

The presence of alkaline salts, especially carbonate of soda, assists in the emulsifying of fat.

Fats are chemically neutral, but if rancid they are acid; if carbonate of soda be added to a fat containing even a small proportion of free fatty acid, the fatty acid unites with the alkali and forms a soap; this soap envelops the fat globules and a true emulsion results.

If the fat acted upon be a neutral fat, nothing less than a free alkali, such as caustic potash, can liberate the fatty acids.

Pancreatic juice, however, can attack perfectly neutral fats, splitting them up into free fatty acids and glycerin, and this it is enabled to do by means of the fat-splitting ferment it contains.

The most important action on the fat is probably the formation of the minute oil globules or emulsionizing, by which means rapid absorption through the intestinal villi occurs.

Colin's experiments on horses and other animals, showed that fats were as perfectly absorbed from the intestine in the entire absence of pancreatic juice as in its presence. This is probably due to the alkaline intestinal fluid.

The ferments of the pancreas which bring about all the changes we have described do not exist ready formed in the gland, but they are formed from a mother-substance termed Trypsinogen, which is manufactured in the cells of the gland. This zymogen by decomposition yields the ferments.

The changes occurring in the cells of the gland correspond very closely with those we have described in the salivary secretion. There is a period of rest during which the gland is rapidly forming the mother-substance of the ferments, which can be seen as minute granules filling the cells, and there is a period of activity during which the gland is discharging its manufactured products. In the herbivora the gland is practically constantly secreting, but the periods of rest and activity still occur for the reason that all the lobes are not active at the same time.

When a pancreas or lobe of a pancreas has been some time at rest the cells forming it are rendered very indistinct, the lumen of the alveolus is nearly obliterated by the swollen

condition of the cells, and the latter are seen crowded with granules which are so arranged as to form on the margin next the basement membrane a clear or fairly clear zone, and within this an intensely granular zone. When activity commences the granules appear to pass centrally towards the alveolus, leaving the cell comparatively clear, excepting that portion immediately abutting on the alveolus, which, even in the exhausted condition, is still granular. These changes have resulted in the cells becoming distinct and clearly defined from each other, and moreover, as they have emptied their granular contents into the alveolus as pancreatic secretion they have consequently become much

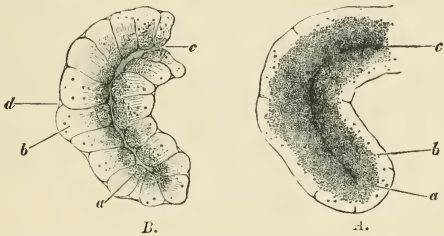


FIG. 11.—A PORTION OF THE PANCREAS OF THE RABBIT (KÜHNE AND SHERIDAN LEA). A, AT REST; B, IN A STATE OF ACTIVITY.

a, The inner granular zone, which in A is larger, and more closely studded with fine granules, than in B, in which the granules are fewer and coarser. *b*, The outer transparent zone, small in A, larger in B, and in the latter marked with faint striæ. *c*, The lumen, very obvious in B, but indistinct in A. *d*, Indentation of the junctions of the cells seen in the active but not in the resting gland (FOSTER).

smaller; the narrow clear zone seen in the resting gland now becomes a broad, clear one, the choked alveolus becomes readily defined, whilst the nucleus of the cell hidden in the charged condition, is now clearly seen. These changes have been worked out on the pancreas of the living rabbit by Kühne and Sheridan Lea (see Fig. 11).

Amount of Secretion.—From the investigations of Colin and others we know that in the herbivora the secretion of pancreatic juice is continuous, though not uniform, reach-

ing its maximum in ruminants towards the end of rumination, when the secretion may attain the rate of 7 ozs. to 9½ ozs. per hour; in the horse the hourly secretion was found to be about the same; and in the sheep about ¼ oz. per hour.

There is no ratio between the size of the animal, the weight of the gland, and the amount of pancreatic fluid secreted; for example, carnivora secrete more than herbivora.

The pressure under which the pancreatic juice is secreted is low; it is said to be equal to ·67 inch of mercury, which is very little greater than that of the bile.

Nervous Mechanism.—Of this nothing is known; the gland is supplied by the vagus and sympathetic. It is probable that a mechanism exists, allied to that found in the salivary glands, but of this nothing is definitely known. The head centre for the pancreas lies in the medulla. The action of pilocarpine and atropine on the secretion is the same as in the salivary glands; the former increases the flow, the latter stops it entirely.

CHAPTER IX.

ABSORPTION.

Lymph.

The methods by which the lymph in the body passes out of the bloodvessels into the tissues, are generally considered in conjunction with the physical process of the diffusion and filtration of fluids. It is more than probable that these may assist in the passage of fluid from the blood into the tissues, yet neither of such purely physical processes is capable of wholly explaining the many facts in connection with lymph formation, and it is therefore more in agreement with advanced physiological thought to attribute its formation to changes in the walls of the capillary bloodvessels, the epithelium of which is probably as intimately concerned in the production of lymph from the blood, as the other cells of the body are concerned in the manufacture of secretions.

The tissues are bathed in lymph, which is contained in the lymphatic spaces which exist between the capillary bloodvessels and capillary lymph-vessels. There is a constant passage of material from the blood into the tissues, and from here through the capillary lymphatics into the main lymphatics, and thence through the thoracic duct into the venous system.

The largest lymph-spaces in the body are the pleural and peritoneal cavities; both these communicate with lymphatic vessels, many of which are in the diaphragm.

Lymph may be regarded as the material by which the tissues are directly nourished; but besides this it may be looked upon as a means by which effete material is col-

lected from the tissues and taken back into the blood. There are certain non-vascular tissues, such as the cornea, where the lymph circulation is the only means by which the part is supplied with nourishment. Speaking generally, however, the lymphatic system may be described as the drainage system of the body, in contradistinction to the blood or irrigating system.

Lymph is a slightly yellow-coloured fluid, alkaline in reaction, with a specific gravity of 1012 to 1022, and possessing the power of spontaneous clotting. The clot it yields is not so firm as that of blood, and takes longer to form; moreover, the bulk of fibrin is much smaller. Lymph may be regarded as blood minus the red corpuscles: it contains, therefore, the proteids of that fluid, cells resembling the white cells of the blood, extractives, salts, and gases. The fluid in which these are contained may be spoken of as lymph-serum. The gases consist principally of CO_2 (which is greater than in arterial, but less than in venous, blood), a small quantity of nitrogen, but no oxygen.

The **Lymph Cells** possess amœboid movements, and are identical with white blood cells. They are more numerous in those vessels which have passed through lymphatic glands, as it is these latter which principally add the corpuscles to the lymph. The cells consist of proteids, lecithin, cholesterin, and fat, and their nuclei contain nuclein. Owing to their power of movement, they are able to pass through the bloodvessels into the tissues and *vice versâ*. The proportion of lymph corpuscles to fluid is about the same as the proportion of white corpuscles to blood.

In the lymph plasma is found the fibrin factors, hence the power the fluid possesses of spontaneous clotting.

Amongst the extractives some observers have found urea, which is said to be always present in the cow; more urea exists in lymph than in blood (Halliburton). The salts are distributed much as those in blood, viz., potash and phosphoric acid in the corpuscles, and soda in the serum.

The lymph corpuscles originate in the lymphatic glands,

the mucous membrane of the intestines, the red marrow of bone, and in the spleen. In the body they undergo decay and death, and are then broken up and help to form the fibrin factors (Landois and Stirling).

ANALYSIS OF THE LYMPH OBTAINED FROM THE LYMPHATICS OF A HORSE* (C. SCHMIDT).

Constituents in 1,000 *parts.*	I.	II.
Water	963·93	955·36
Solid matters	36·07	44·64
Fibrin		
Albumin	28·84	34·99
Fats and fatty acids		
Other organic matters		
Inorganic matters	7·22	7·47
Sodium chloride	5·43	5·67
Sodium	1·50	1·27
Potassium	0·03	0·16
Sulphuric acid	0·03	0·09
Phosphoric acid combined with alkalies	0·02	0·02
Calcium and magnesium phosphate	0·22	0·26
In the serum from 1,000 parts of lymph Schmidt found :		
Albumin	23·32	30·59
Fats and fatty acids		1·17
Other organic matters	4·48	1·69

ANALYSIS OF THE LYMPH OF A COW (C. SCHMIDT) :

Serum	95·52
Clot	4·42

	In 100 *parts serum.*	*In* 100 *parts clot.*
Water	95·76	90·73
Fibrin	—	4·86
Other albumins	3·20	—
Fats	0·12	3·43
Organic matter	0·17	—
Salts	0·74	0·96
Sodium chloride	0·56	0·60
Soda	0·13	0·06
Potash	0·01	0·10
Sulphuric and phosphoric acids and earthy phosphates	0·04	0·23

* I am indebted for these analyses of lymph and chyle to Gamgee's 'Physiological Chemistry' and Colin's 'Physiologie Comparée.'

Here is an analysis comparing lymph with blood:

	Lymph (Wurtz).		*Blood (Nasse).*	
	Ox.	*Cow.*	*Ox.*	*Calf.*
Water	938·97	955·38	799·590	826·440
Fibrin	2·05	2·20	3·620	5·737
Albumin and extractives	50·90	34·76	66·901	56·414
Fats	0·42	0·24	2·045	1·610
Salts	7·46	7·41	7·041	8·241
Blood corpuscles			121·865	102·803

It can be easily understood that the chemical composition of the lymph will depend upon the nature of the food supplied, and also the sources from which the lymph is obtained. The following table illustrates the differences in the lymph of the horse, depending on its source:

	Lymph collected from the Femoral Vessels. (Gmelin.)	*Lymph collected from the Cervical Vessels. (Lenoir and Lassaigne.)*	*Lymph collected from the Vessels of the Foot. (Geiger.)*	*Lymph from the Vessels of the Foot of an Ass. (Reed.)*
Water	964·30	925·00	983·70	965·36
Solids	35·70	75·00	16·30	34·64
Fibrin	1·90	3 30	0·40	1·20
Albumin and Extractives	23·17	57·36	8·90	27·59
Fats	traces		traces	traces
Inorganic matters	10·63	14·34	7·00	5·85

The **Quantity of Lymph** in the body is very difficult to arrive at, and varies considerably; 13¼ lbs. of lymph have been collected in two hours from a lymphatic vessel in the neck of a horse (M. Smith). Landois mentions that 2½ ozs. to 3½ ozs. have been collected from the same place in 1½ to 2 hours. Colin obtained from a lymphatic in the neck of horses a quantity which varied between 1 to 4 lbs. in 24 hours; the mean amount was 2 lbs. 6 ozs. for the same period, but he notes that the variations are very wide, and that herbivora secrete more than carnivora, and young animals more than adults. The amount of material col-

lected from the thoracic duct of a cow in 24 hours has been found to be 209 lbs.! but this is no guide to the quantity of lymph in the body, as the material in the thoracic duct is mixed with the chyle from the intestines. It is usual, however, in this vessel to consider two-thirds of the contents to represent chyle and one-third lymph. The quantity of mixed chyle and lymph obtained by Colin some hours after the animals had been fed is as follows:

Horse, 30 lbs. to 90 lbs. in 24 hours.
Oxen, 46 lbs. to 209 lbs. in 24 hours.
Sheep, 6½ lbs. to 10 lbs. in 24 hours.

The amount of lymph in the tissues is increased by the activity of the parts, by increase in the blood pressure, and by obstruction or otherwise to the free passage of lymph back to the general circulation. As a rule, no more lymph bathes the tissues than can be carried off by the capillary lymphatics. If the irrigation exceeds the drainage capacity œdema results.

It should be noted that excessive transudation is a more potent factor in the production of œdema than defective drainage. This excessive transudation may be brought about by obstructed venous flow (more lymph passing into the spaces than the latter can get rid of), or by changes in the character of the blood permitting it to pass through the walls of the capillaries; this is well exemplified in anthrax and inflammatory œdema of the horse.

The method by which the lymph passes from the blood-capillary into the lymph-space is termed transudation. We have before mentioned that certain physical processes, such as osmosis and filtration, may assist in the production of lymph, but it is to the blood pressure and the wall of the vessel that the chief results are to be attributed. When the lymph has passed into the lymph-space, its next movement is towards the capillary lymph-vessel, and the methods by which this is accomplished are probably by passages which exist between the space and capillary, and not by transudation, or, in other words, not by any purely physical

process such as is assumed by some observers, who have not been able to trace any communicating channels, paths, nicks, or crannies between the lymph-space and the capillary.

The lymph having now reached the capillaries from the spaces, we have next to consider how it is pressed onwards so as to reach the thoracic duct.

The **Movements of the Lymph** are due partly to the blood pressure in the arteries at the seat of the formation of lymph, which, with certain factors now to be mentioned, forces the fluid from the lymph-spaces to the thoracic duct. The pressure in the lymphatic of a horse has been ascertained by Weiss to be ·4 to ·78 inch of mercury. There is a gradual fall of pressure from the tissues to the duct. Muscular contractions also mechanically favour the passage of the lymph, the vessels for which are provided with valves, which prevent the fluid from flowing backwards; the obstruction caused by the lymphatics passing through the various glands must be considerable, yet these latter, by means of the contraction of their covering of involuntary muscular fibre, more than compensate for the obstruction caused by the gland itself. Once the lymph has found its way into the thoracic duct, its passage into the general circulation is not only favoured by gravity, but also by the negative pressure produced in the jugular vein by the process of inspiration, the result being that the lymph is aspirated out of the duct into the vessel. This aspirating influence has been proved by experimental inquiry, a negative pressure having been observed during inspiration, though a positive pressure of ·5 inch of mercury exists in the thoracic duct of the horse during expiration. That this is not due to the positive pressure in the jugular vein is certain, for the latter is prevented from forcing blood into the thoracic duct by the presence of a valve, which only allows fluid to pass from the duct into the vein.

The lymph moves slowly in its vessels. Weiss has observed 9 inches to 11 inches per minute in a large lymphatic in the neck of a horse.

The movements of the diaphragm, tendons, and fasciæ produce an aspirating effect on the lymph circulating through them. In the case of the diaphragm the lymphatic vessels drain the two large lymphatic sacs—the pleura and peritoneum. Owing to the direction taken by the fibrous tissue of the diaphragm, compression is exerted on the lymph-spaces during its contraction, forcing the fluid onwards, whilst a sucking action is produced when the part relaxes by which the vessels are filled. This pumping arrangement exists in tendons, fasciæ of muscles, etc., and is a valuable aid in lymph circulation. The swollen condition of the legs of horses standing idle is due to lymph stasis; hence the value of hand-rubbing and bandaging the limbs, exercise, etc., as methods of treatment.

The whole of the lymph in the body, excepting that from the right side of the head, neck, and off fore-leg, is collected and poured into the thoracic duct, which empties itself into the left jugular vein; the other parts above mentioned are drained by vessels emptying themselves into the right jugular vein. In both cases the part of the vein penetrated is close to its bifurcation.

There is no special system of nerves known as governing the lymphatic vessels and spaces.

Chyle.

In the thoracic duct the lymph from the body meets with the lymph coming from the intestines, termed here chyle. Chyle is closely allied to lymph in its chemical composition, but it differs from it in containing a quantity of neutral fat, which gives it its milky appearance. The fat is in the condition of fine particles, owing to the emulsifying process it has undergone in the intestines before passing into the villi. The particles of fat are remarkable for their small size; these give to chyle what is known as the molecular basis. It is this molecular basis which distinguishes chyle from lymph.

The following analyses of chyle will give an idea of its composition:

Analyses of Chyle of the Horse (Hoppe-Seyler).

Constituents in 1,000 parts.	I. *Chyle of Horse.*	II. *Chyle of Horse.*	III. *Blood-serum of Horse.*
Water	960·97	956·19	930·75
Solids	39·03	43·81	69·25
Fibrin	2·57	1·27	—
Albumin	22·60	29·85	56·59
Fat, cholesterin and lecithin	0·09	0·53	—
Fatty acids in the form of soaps	0·76	0·28	1·57
Other organic matters	5·37	2·24	3·85
Hæmatin	0·05	0·06	—
Mineral salts	7·59	7·49	7·14
Sodium chloride	5·76	5·84	5·74
Sodium	1·31	1·17	0·87
Potassium		0·13	0·14
Sulphuric acid	0·07	0·05	0·11
Phosphoric acid	0·01	0·05	0·01
Calcium and magnesium phosphates	0·44	0·25	0·26
Carbonic acid	1·02	0·82	0·56

Chyle from the Thoracic Duct (Wurtz).

	Ox.		Cow.	Cow.
	Before Rumination.	*After Rumination.*	*Fed with Hay and Straw.*	*Fed with Straw and Clover.*
Water	950·89	929·71	951·24	962·21
Fibrin	1·76	1·96	2·82	0·93
Albuminoids	39·74	59·64	38·84	26·48
Fats	0·81	2·55	0·72	0·49
Salts (soluble in alcohol)	2·47	2·50	2·77	1·92
Salts (soluble in water)	4·33	3·61	3·59	7·97

Chyle contains more solid material than lymph, and, as mentioned above, very much more fat. Though the proteids are absorbed as peptones, yet no peptones are found in chyle, owing to the fact that these pass away by the

bloodvessels, after undergoing a change in the intestinal wall which we shall presently indicate. It is said that no sugar, or but very little, is taken up by the lacteals from the bowels, the bulk of the carbo-hydrates being carried off by the portal vein to the liver; but Colin states that sugar is found in the chyle of the horse, ·12 to ·14 per cent., and that this amount is increased by the introduction of glucose into the bowels.

The gases in chyle are much the same as in lymph, viz., a considerable quantity of carbonic acid, a little nitrogen, and a mere trace of oxygen.

The composition of chyle varies with the nature of the food; on a hay diet the fat is small, but when fed with oats the amount of fat increases considerably. I have not been able to obtain chyle from the horse that is not slightly reddish in tint; its reaction is alkaline, and the specific gravity varies from 1007 to 1022. In starving animals, the chyle is more transparent than when collected after a meal. Colin observes that the chyle of herbivora is yellowish or yellowish-green, very slightly opalescent, and in appearance like turbid milk. He also says that the chyle of starving animals, besides being limpid and transparent, has almost lost its coagulability.

The chyle while passing upwards through the mesenteric glands has added to it certain formed elements—lymph corpuscles—and now possesses the power of spontaneous clotting.

The movement of chyle is due to the muscular contraction of the villi forcing the chyle onwards, the valves in the lacteals preventing its return. Intestinal peristalsis may also assist, and the negative pressure in the thoracic duct during inspiration must largely help in aspirating the contents of the chyle vessels upwards.

Absorption in General.

The activity of absorption in the horse has been made known to us by the experiments of Colin.

Absorption from the Respiratory Passages is remarkably

rapid. Stimulated by Colin's researches, I have for years administered certain alkaloids by the trachea rather than by the skin.* Colin showed that potassium ferrocyanide could be detected in the blood 2 minutes after being injected into the trachea, and that it appeared in the blood before it was found in the chyle. The same salt was also found in the urine 8 minutes after being introduced into the trachea. A solution of nux vomica injected into the trachea produced tetanic symptoms in 3 minutes; turpentine, alcohol, and ether were also rapidly absorbed, but oil could not be taken up, and it was rejected by the nostrils.

Such drugs as morphia, pilocarpine, physostigmin, etc., are all rapidly absorbed; according to my observations they produce their therapeutical effect in a shorter time than when simply injected under the skin. The absorption of water from the trachea is also remarkably rapid. Colin introduced 6 quarts of water per hour into the trachea of a horse; the animal was destroyed at the end of $3\frac{1}{2}$ hours, and no fluid was found in the bronchi; he also poured into the air-passages one pint of water at a time, repeating this without intermission: in this way he poured in 74 pints of water before he caused death. A horse may be placed under chloroform almost instantaneously by an intra-tracheal injection of the drug.†

The rapidity of absorption from the respiratory passages is therefore remarkable; and, further, the lungs have the power of absorbing certain poisons like curare, which are not absorbed when introduced into the digestive canal.

Absorption from the Cellular Tissue is very active; ferrocyanide of potassium injected into the face was detected in a carotid lymphatic in 7 minutes, though in order to

* It is interesting to observe that the injection of liquids into the trachea (either high up or as low as its bifurcation) excites the reflex act of swallowing, probably due to stimulation of the recurrent or other laryngeal nerve.

† It is not intended here to recommend the intra-tracheal administration of chloroform.

reach this place the salt had to pass through the sublingual, parotid, pharyngeal, and tracheal lymphatic glands. The rapidity of cellular tissue absorption is hastened by muscular movement.

Absorption from the Conjunctiva is very pronounced for some drugs and certain organic poisons, but there are other drugs and poisons which are not absorbed in this manner. Curare is not absorbed through the conjunctiva, and Colin could not infect horses with anthrax by placing anthracoid blood and fluids in the conjunctival sac.

Absorption by the Skin is slow, even for those drugs which will pass through it, and there are many organic and inorganic substances which refuse to pass through the unbroken epidermis. Colin kept the lumbar region of a horse wet for 5 hours with a solution of ferrocyanide of potassium. The salt was detected in the urine in 4½ hours, although the skin was quite unbroken. From a wound or abraded surface absorption will occur rapidly with some agents, slowly with others. The above observer placed a horse's foot, with a wound on the coronet, in a solution of ferrocyanide of potassium; in 20 minutes he detected the salt in a lymphatic of the thigh. In connection with absorption from a wounded surface, he found that the poison was taken up quite as readily by the lymphatics as by the bloodvessels. The mucous membrane of the vagina only absorbs very slowly.

Experiments made on **Absorption from the Pleural and Peritoneal Cavities** showed that such drugs as strychnine rapidly produced fatal symptoms when injected into these sacs; even in such a short time as from 3 to 7 minutes tetanic symptoms supervened. Potassium iodide injected into the peritoneal cavity of a sheep was detected in the thoracic duct 5 to 8 minutes after the operation. When we consider the numerous connections these large lymphatic spaces have with the lymphatic system, the rapidity of absorption cannot be wondered at.

Some colouring matters are readily absorbed by serous membranes.

Intestinal Absorption.

The remarkable fact that no absorption occurs from the stomach of horses (see p. 134) points to intestinal absorption as being of considerable importance. That this absorption is very rapid is proved by Colin's experiments. Hydrocyanic acid injected into the small intestine of a horse caused death in 1 to 1½ minutes, and potassium ferrocyanide injected into the bowel, after tying the lymphatics, may be detected in the blood 6 minutes later.

The Paths of Absorption.—The paths by which intestinal absorption occurs are (1) through the villi into the lacteals, and (2) through the bloodvessels into the venous system.

The villi are found only in the small intestines; they are ·04 to ·07 inch long, and possess a diameter of from ·02 to ·04 inch. They are comparatively small in herbivora, and their number in the horse and ox, according to Colin, is from 45,000,000 to 55,000,000, and these are distributed over a surface of from 48 to 58 square feet. The lacteals pass up the mesentery, and each of the 1,200 vessels counted by Colin passes through a lymphatic gland before gaining the receptaculum chyli; here the chyle mixes with the lymph coming from the posterior extremities, and the whole is passed into the left jugular vein.

The material absorbed by the bloodvessels passes into the portal vein and reaches the liver before entering the general circulation. This arrangement would point to the fact that there are certain substances which need only pass through a lymphatic gland before being suitable for the blood, whilst others must pass through or undergo changes in the liver previous to being rendered suitable for the system. Physiologists have therefore devoted considerable consideration to this subject, but it is far from being in a satisfactory condition. In the large intestines there are practically no villi. It must not, therefore, be supposed that absorption is here exclusively carried on by the bloodvessels; for, remembering the large chain of glands along the colon in particular, it is probable that the material absorbed passes through these glands to a greater or less

extent, as in the mesentery, before entering the circulation. There is, at any rate, a well-developed lymphatic system in the walls of the large intestines; it is possible, therefore, that material is taken up in the large intestines both through the bloodvessels and lymphatics, and that this absorption is something considerable may be readily understood when we remember the size of these bowels and the nature of their contents; in the cæcum, for instance, the contents are fluid, derived largely from the water consumed, and we know that this is readily taken up into the system, the path in this instance being probably exclusively by the bloodvessels.

Absorption from the large intestines is active; we have given reasons for believing that it may be lymphatic as well as capillary. That substances can be taken up with extreme rapidity from the large bowels is a well-known fact; anæsthetics, such as ether, may be administered to the horse per rectum. Colin observed that 18 minutes after injecting a solution of nux vomica into the cæcum convulsions began, and 8 minutes later the animal was dead.

The absorbent surface of the large intestines is equal to 75 square feet, and, according to Colin, each square yard collects 16½ lbs. of solid and liquid matter in 24 hours in both horse and ox. This observer gives a table showing the solid and liquid material poured into the intestinal canal in 24 hours, from which we may judge that the enormous absorbent surface to which it is exposed is none too large:

Diet	26	lbs.
Water consumed	66	„
Saliva	92½	„
Gastric juice	11	„
Bile	11	„
Pancreatic juice	11	„
Intestinal juice	22	„

Returning, however, to the small intestines, it has been observed by Colin that in the horse, almost immediately after food has been given, waves of chyme are passed into the duodenum, and at once the lacteals in the mesentery in

connection with this portion of intestine become opaque, though previously they were filled with a colourless fluid. As the chyme passes along the bowel the other lacteals in their turn become opaque, until at last the whole of them are filled with this milky fluid. Colin draws especial attention to this regular invasion of the lacteals from the duodenum to the ileum.

The various principles of the food having been rendered fit to be taken up into the system, by what channels is this accomplished?

Absorption of Fat.—Experimental inquiry, limited almost entirely to dogs, points to the lacteals as the means by which the fatty part of the food is taken up. It has been observed that these vessels after a diet rich in fat are filled with a milky fluid rich in the same substance, whilst the blood in the portal vein does not contain more fat than that of any other vein in the body. Clearly, therefore, in dogs at least, the lacteals take up the fat. But what about herbivora, the diet of which contains but little fat, that of the horse in particular? Exactly the same appearance of milky lacteals is obtained in the horse after feeding on a diet notoriously deficient in fat; it is possible, therefore, that in the horse the lacteals may take up other substances than fat, and that the milky appearance is not due to fat alone. The absorption of fats is not perfect, for even in dogs only about 60 per cent. of the fat eaten can be recovered from the thoracic duct, and none, as we have mentioned before, enters the blood.

Colin expressly states that proteids and sugar are also absorbed by the lacteals in the horse, and on this point I am certainly inclined to agree with him, in spite of experiments to the contrary on dogs. This observer injected glucose into the intestine, and the chyle contained in a short time a decided increase in sugar.

Returning to the question of fat absorption, we observe that by the action of the epithelium covering the villi the minute fat globules forming the emulsion are drawn in and passed on to the lacteals; from here they ascend the

mesentery, passing through the mesenteric glands, where certain additions are made to the stream in the shape of cells, and the whole is poured into the general circulation. It is a well-known fact in human surgery that fat embolism is not an infrequent accompaniment of certain injuries, fractures, etc. The fat of the body is taken into the blood-vessels and blocks the capillaries, especially those of the lungs. Fat embolism in lacteal absorption is prevented by the fine emulsion produced in the intestines, for no emulsion can occur in any other part of the body, in spite of the alkaline nature of the blood, owing to the fact that the body fat is neutral, and neutral fats can only be emulsified by free alkalies, and not by their carbonates (Bunge).

Absorption of Sugar.—The sugar formed in the bowel is said to reach the general circulation *viâ* the portal vein and liver. We have reason, however, to believe that some portion of it may find its way into the lacteals; but the bulk of it must of necessity be absorbed by the blood-vessels, and pass by the portal vein into the liver. We have seen, in speaking of the liver, how important is the function of this gland in regulating the supply of sugar to the system, and the method it possesses of storing it up.

The **Absorption of Proteids** is said to be exclusively by the bloodvessels, from whence they are conveyed to the liver by the portal vein; but here a curious point arises: little or no peptone can be found in the portal vein or even in the general mass of blood. If peptone be experimentally injected into the blood it is rapidly excreted by the kidneys, so that it is evident the peptone taken up from the intestinal canal must undergo some important and rapid change before entering the portal system. Hofmeister's work in this direction has shown that the peptone is converted once more into proteid, and that this change occurs in the intestinal mucous membrane, so that peptones enter the system in the form of proteid. The process is analogous to that we have previously dealt with in speaking of glycogen, where the starch enters the blood as sugar, but is

again converted into a kind of starch in the liver; from here it is converted into sugar for the use of the blood. Similarly the proteids are converted into peptones in the intestine in order that they may be more readily absorbed into the intestinal walls, but they are no sooner in the capillaries than they are found to be proteid once more.

The blood of the portal vein does, however, contain a small portion of peptone, which appears to have escaped this conversion; but instead of passing out of the blood by means of the kidneys, as injected peptones do, it is enabled to circulate in the stream by being lodged in the white cells of the blood, and Hofmeister and his pupils have shown that the number of white blood cells depends upon the proteid matter in the food, and is not affected by carbo-hydrates, fats, salts, or water.*

* Bunge.

CHAPTER X.

THE SKIN.

It is obvious that one important function the skin performs is that of affording cover to the delicate parts beneath, and wherever the chance of injury is the greatest we generally find the skin is the thickest, whilst in those parts where sensibility is most required the skin is thinnest. The skin of the back, quarters, and limbs are good examples of the first type; on the back especially we have a protective covering which, in some horses, is as much as a quarter of an inch in thickness. The face and muzzle is a good example of the latter variety, the skin in some parts being as thin as paper. In those parts not exposed to violence we also find the skin thin, as on the inside of the arms and thighs.

According to Colin, the surface of the horse's skin is equal to from 50 to 60 square feet.

The skin as an organ of touch is of great importance. All animals appear most sensitive to slight skin irritation; flies will cause horses to go nearly mad with irritation, and the elephant, with his thick hide, is quite as sensitive to these tormentors as a highly-bred horse.

The skin is highly endowed with sensory nerves, particularly in those parts connected with the organs of prehension, where also the long hairs growing from the part are brought into contact with distinct nerve-endings.

The skin is a bad conductor of heat, and this is considerably assisted by the layers of fat found beneath it or at no great distance from it, as in the abdominal region, where the subperitoneal fat protects the viscera of animals living in the open and lying in wet places.

The epidermal covering of the skin relieves the part from excessive sensitiveness, such as would occur to an exposed sensory surface, and through the sebaceous secretion it assists in preventing loss of heat, whilst the greasy covering throws off the rain, prevents the penetration of water, and thus saves the epidermis from disintegration.

By means of the hair growing from the skin the heat of the body is maintained and prevented from passing off too rapidly. The thickness of the hairy covering varies considerably with the class of horse: the better bred the animal the finer the coat. I have obtained from draught horses between 7 lbs. and 8 lbs. of hair by clipping; in a well-bred horse this would be reduced to 10 ozs., or even less.

It is a well-known fact that, excepting the hair of the mane and tail, that of every other part of the body has only a temporary existence, and is changed twice a year—once for a thick, and once for a fine coat. It is found that the heavy coat grown by horses is the cause of considerable sweating at work, and the general practice of clipping has been introduced. Of its value there can be no doubt: it considerably reduces the risk of cold and chest disease, for animals, instead of coming in from work with a wet skin—which in some cases will not dry for hours—are readily dried and easily protected against inclement weather.

Animals which sweat freely at work lose condition. I have shown that this is due to the proteid lost by the skin, for, as we shall presently see, proteids are regularly found in the sweat of the horse; clipping largely prevents this loss. As to the influence of clipping on temperature, see 'Animal Heat.'

The loss of epidermis by the skin from grooming and other causes is something considerable, and is an explanation of the nitrogen deficit met with in experiments on the body-waste. The amount of epidermis lost during an ordinary grooming will vary considerably, depending on the cleanliness of the animal and the state of the coat; in fairly clean horses it has amounted to between 25 to 60 grains, and in very dirty animals from 170 grains to 220 grains.

As epidermis largely contains sulphur, this is one channel of removing it from the body.

By means of the glands in the skin we find secreted an albuminous fluid termed 'sweat,' and a fatty material known as 'sebum.'

Sweat, or perspiration, is not found to occur over the general surface of the body in any other hairy animal than the horse. It is said that sheep perspire (?), the ox to a less extent and principally on the muzzle, and the dog and cat on the foot-pads.

The sweat exists in two forms: viz., the invisible vapour which is always rising from the surface of the skin, and distinguished as the 'insensible perspiration'; and the visible material, which is termed 'sweat.'

Colin gives various figures representing the insensible perspiration, from which we gather that 14 lbs. of water probably represents this loss in the horse for 24 hours. Much depends upon the humidity of the atmosphere: the drier it is the greater the insensible perspiration.

Sweat obtained from the horse by scraping is always alkaline—strongly so; after filtration it is the colour of sherry, and possesses a peculiar horse-like odour, with a specific gravity of 1020. One specimen examined by me gave the following analysis:*

Water	-	-	94·3776		
Organic matters	-	-	·5288	Serum albumin	- ·1049
				„ globulin	- ·3273
				Fat - -	- ·0020
Ash	-	-	5·0936	Chlorine	- ·3300
				Lime -	- ·0940
				Magnesia	- ·2195
				Phosphoric acid	- traces
				Sulphuric „	- „
				Soda -	- ·8265
				Potash	- 1·2135

The proteids are thus seen to be serums albumin and globulin, and their constant presence has been determined by a number of observations. The mineral matter is very

* *Journal of Physiology*, vol. xi., No. 6.

high and consists of soda and potash, especially the latter. It will be observed that the mineral matter exceeds the organic matter, and in horses which have sweated freely the matted hair (which is due to the albumin) is often seen covered with saline matter, looking like fine sand. In the paper referred to I have shown that there appears to be some complemental action between the skin and the kidneys in the elimination of soda and potash; during rest the kidneys eliminate these salts, whilst during work they are assisted by the skin.

It is difficult to see why horses should excrete albumin by the skin.

The secretion of sweat in the horse is governed by some different nervous apparatus to that which exists in man and other animals. I am not prepared to state what this difference is; it may only be a slight one, but it manifests itself in the action of pilocarpine, which has absolutely no effect on the sweat glands of the horse, though it produces the most profuse salivary flow.

The peculiar breaking out into sweats which occurs in horses after work has no parallel in man; nothing is more common after a horse has been perfectly dried than to find him break out two or three times into a sweat, which leaves him as wet as he was originally.*

We have no drug which can excite the sudoriferous secretion in the horse; this is an explanation of the common use of nitre in veterinary practice: we make the kidneys do what the skin is unable to. All this points to some difference in the nervous arrangement, but until these differences are ascertained we may provisionally adopt, as the probable changes in the glands during sweating, the results obtained on the sweat glands of carnivora.

Sweating is produced by the action of the nerves supplying the vessels of the sweat gland, and by special secreting fibres supplying the gland itself; under ordinary circumstances these work together, the bloodvessels dilate and the secreting fibres are active; but it is not essential to

* I have also observed sweating to occur immediately after death caused by shooting through the head.

the secretion that the vaso-dilator fibres should be in operation, for we know that sweating will occur in a nearly bloodless skin, as in the cold sweats following on ruptures of such viscera as the stomach; and against this we have the fact that in many cases of arterial thrombosis of the hind limbs the sweat is pouring off the general surface of the body (probably from pain), whilst the quarters and hind extremities remain dry.

The special secreting fibres supplying the cells of the sweat glands have centres in the cord for the body and limbs, and in the cervical sympathetic for the head. There is also, probably, a sweat centre in the medulla. Dupuy divided the cervical sympathetic of the horse, and obtained sweating of the head and neck on the operated side.*

The changes occurring in the secreting cells of the sudoriferous glands of the horse are described by Renaut.† When charged the cells are clear and swollen, the nucleus being situated near their attached ends; when discharged they are smaller, granular, and their nucleus more central.

The amount of sweat secreted daily can only be roughly guessed at: there are many conditions which affect it, such as the length of coat, nature of the work, and pace. I should think a minimum secretion would be about 1 pint, and this I arrived at by brushing a horse lightly over with water.

Doubtless the compensating action existing between the kidneys and skin observed in men exists also in the horse, viz., when the skin is acting freely less water passes by the kidneys, and *vice versâ*.

Sebaceous secretion or sebum is very extensive in the horse; its action is protective to the skin. The glossy coat, which is due to the natural skin fat, throws off a considerable amount of water before penetration occurs.‡ In certain places, as in the prepuce, considerable quantities of this secretion are found. The sebaceous secretion of the prepuce of the horse consists of 50 per cent. fat, and also contains calcium oxalate (Lehmann).§ The secretion of

* Landois and Stirling. † Quoted by Halliburton.

‡ I have found that the dandruff removed from horses by grooming contains a large quantity of fat. § Quoted by Halliburton.

smegma is very considerable in the horse. The ear-wax and eyelid secretion is also of a sebaceous nature.

In the sheep a considerable quantity of fatty substance is found in the wool: it exists in two forms, (1) as a fatty acid united to potash to form a soap, and (2) a fatty acid combined with cholesterin instead of glycerin: the latter is known as lanolin, and is largely used as a basis for ointments. It is also found in hair, horn, feathers, etc.

The fatty substance in the fleece is known to shepherds and others as 'suint'; in merino sheep it may amount to more than one-half the weight of the unwashed fleece, but in ordinary weather-exposed sheep it may be 15 per cent. or less. The large amount of potash in unwashed wool is very remarkable; a fleece must sometimes contain more potash than the whole body of the shorn sheep (Warrington).*

The respiratory function of the skin, so marked in the frog, is not very active in the higher animals: CO_2 passes out and O passes in through the skin. The amount of the latter for the horse, so far as I am aware, has not been determined; it is probably very little.

Gerlach† is said to have collected $\frac{1}{2}$ oz. of carbonic acid in 24 hours from the skin of horses at rest, and 3 ozs. at work; it is difficult to know how these figures were arrived at unless the horse were enclosed in a rubber bag.

Varnishing the skin will rapidly cause death in rabbits, and more slowly in horses. Death is due to loss of body heat, and not to suffocation as was at one time supposed. Horses shiver when varnished, and the surface of the body and expired air become cold, the visible membranes are violet, and the animals die after several days (Gerlach,‡ Bouley§); but according to Ellenberger, if only partly varnished they do not die, but exhibit temporary loss of temperature, and show signs of weakness.

For absorption from the skin, see article 'Absorption,' p. 185.

* 'The Chemistry of the Farm.'

† Quoted by M'Kendrick.

‡ Landois and Stirling.

§ Colin.

CHAPTER XI.

THE URINE.

It is usual to speak of the urine as a secretion, but this is not strictly correct; speaking broadly, we may say a secretion is something which is formed in a part for the purpose of being eventually utilized by the system. This does not apply to the urine, the chief ingredients of which are not even formed in the kidneys, but only separated by them: moreover, the urine having once been formed is of no further use to the body, and is excreted. An excretion, therefore, is a something removed from the system as being no longer required, and the retention of which would be harmful.

The kidneys may be regarded as the filters of the body, and one of the channels by which waste and poisonous products are removed or filtered off from the blood, by which means the latter fluid is maintained in a healthy condition. We have seen how both nourishment and waste materials are poured into the circulation, and we have studied several of the channels by which the latter are removed, viz., by the lungs, skin, and intestinal canal: we have now to examine the last excretory path, viz., the kidneys.

We regard the kidneys as the means by which the waste products of the body are removed, or by which even normal constituents of the blood are got rid of if in excess; and, according to Bunge, by the selective power which the epithelial cells of the tubules possess, the alkalinity of the blood is maintained, alkali being got rid of or sent back to this fluid as it needs it.

The structure of the kidney is peculiar, inasmuch as that

portion of it which excretes the water does not excrete all the solids; the water is removed from the blood by the Malpighian bodies, the solids are removed from the blood in the tubules: in both cases the epithelial cells which line these parts are the active factors in the matter. The Malpighian body is arranged so that the blood is always at high pressure within it; this is accomplished by the efferent vessels being smaller than the afferent. At this high pressure the watery part of the blood transudes through the epithelium into the capsule surrounding the tuft (known as Bowman's capsule), and thence into the tubules. It has been stated that a certain proportion of proteid also passes through the epithelial wall of the tuft, to be reabsorbed later on in the tubules; but as proteids do not occur in normal urine, we may safely believe that the epithelium of the tuft does not in an undamaged condition allow any to pass. During the passage of the water through the tubule, the secretory cells of the latter pass into it the organic and inorganic material which they have separated from the capillary vessels which surround them, and at the same time it is stated that a portion of the water, of which an excess is excreted in the Malpighian tufts, is reabsorbed.

There are no known secretory nerves of the kidneys; the vessels are under the control of the vaso-motor system, and depending upon whether they be dilated or constricted, so we have an excess or diminished secretion, but no secretory nerves proper are known.

The **Composition of the Urine** depends upon the class of animal. In all herbivora, with certain minor differences, the urinary excretion is much the same, but not so with omnivora or carnivora, which possess, especially the latter, a distinctive urine. When herbivorous animals live on their own tissues, as during starvation, they become carnivora, and their urine alters completely in character, corresponding to the urine of flesh feeders. The young of herbivora, if still sucking, also have a urine possessing much the same properties as that of carnivora.

Urine consists of:

Water.

Organic matter { Nitrogenous end products: urea, uric acid, hippuric acid, creatin, creatinin. / Aromatic compounds: benzoic acid, ethereal sulphates of phenol, cresol, etc. / Colouring matter and mucus.

Salts { Sodium, potassium, calcium, magnesium, combined with chlorine, sulphuric and phosphoric acids.

The **Reaction** of the urine of herbivora is alkaline, the alkalinity being due to carbonate of potash. The urine of all vegetable feeders is alkaline, owing to the combustion in the system of the acid potash salts, the potash appearing in the urine as carbonate, and producing considerable effervescence on the addition of an acid. The nature of the food influences the reaction, for it is stated that the urine of the horse may be rendered acid by feeding entirely on oats. A considerable quantity of the alkalinity present in stale horses' urine is due to the exceedingly rapid change which occurs in it on standing, leading to the breaking up of part of the urea and the formation of ammonia carbonate. The fixed alkalinity of the urine for the twenty-four hours, in the horse is equivalent to the excretion of between 45 grains to 60 grains of potassium oxide.

The following remarks apply solely to the urine of the horse; what is known of this excretion in other animals will be spoken of subsequently.

The **Specific Gravity** of urine varies considerably: the mean of a large number of observations was 1036; the highest registered was 1050, and the lowest 1014.

The **Quantity** of urine for the 24 hours is about 8½ pints; working horses excrete less, owing to the loss by the skin, etc.

In estimating the urinary constituents for the 24 hours, they should always be calculated on the total amount passed, and the sample examined should be a portion of the 24 hours' fluid. Without the total urine it is impossible to estimate the changes in the system. For clinical purposes, where the presence or absence of a substance is

all we wish to know, the examination of a single portion of urine may suffice.

The **Odour** of urine is said to be due to certain aromatic substances of the phenol group. Perfectly fresh urine has a most distinct though faint smell of ammonia.

The normal fluid is always turbid, some specimens more so than others; very rarely is it clear, and then only for a short time. The turbidity is due to the amount of suspended carbonate of lime and magnesia which exists in it; as the urine cools, particularly if it undergoes ammoniacal fermentation, the amount of turbidity becomes intense.

The consistence of the fluid depends upon sex, and perhaps on the season. It is certain that some mares excrete quite a glairy tenacious fluid, which can be drawn out in strings, due to the amount of mucin it contains: it is very common to find it as thick as linseed-oil, and very rare to find it fluid and watery.

Of the total water consumed, about one-fifth passes away in the urine, though Munk* considers that one-third passes away by the kidneys and two-thirds by the lungs. An interesting point is the ultimate disposal of the water consumed by various animals; it has been found that carnivora excrete by the kidneys the greater part of the water they drink, whilst herbivora excrete the greatest part by the lungs.

Here is Munk's table:

Man: 60 per cent. of water escapes by the kidneys, and 40 per cent. by the lungs and skin.

Carnivora: 70 per cent. of water escapes by the kidneys, and 30 per cent. by the lungs and skin.

Herbivora: 30 per cent. of water escapes by the kidneys, and 70 per cent. by the lungs and skin.

The **Colour** of the urine is yellowish-red, rapidly turning to brown, the dark tint commencing on the surface of the fluid and gradually travelling into its depth. The cause of the colour will be dealt with shortly.

* Quoted by M'Kendrick.

The **Total Solids** of the urine consist of organic and inorganic matter, of which 5 ozs. are organic and 3 ozs. inorganic; they are liable to great variation, sometimes being found to be considerably in excess of that mentioned.

The total solids are considerably affected by the diet. E. Wolff* found that when he reduced the hay and increased the corn ration, the solids in the urine decreased; thus, on a diet of 17·6 lbs. hay and 4·4 lbs. oats the urinary solids for 24 hours amounted to 20 ozs., whilst on a diet of 8·8 lbs. hay, 13·2 lbs. oats, the total solids fell to $16\frac{1}{4}$ ozs.

Urea is the chief end product of proteid change; it represents the wear and tear of proteid tissues, but is not, as we shall see in another chapter, a measure of the work produced. The amount of urea excreted daily is about $3\frac{3}{4}$ ozs. Half the weight of urea consists of nitrogen. The sources of urea have given rise to considerable discussion; it was supposed to originate in the muscles, but muscular substance only contains a trace of urea, if any. It is considered that it may be formed in two or three ways: 1. From the nitrogen of the food split off during pancreatic digestion in the form of leucin and aspartic acid, bodies known as the amido acids. 2. But these amido acids do not account for all the urea, and it is supposed that the ammonia and carbonic acid split off from the proteid molecule subsequently combine to form urea. 3. It is possible that creatin, a substance which exists largely in muscle, may undergo conversion into urea.

In whatever way urea is formed the seat of the change is principally in the liver, while probably the spleen and lymphatic glands may participate (Halliburton).

The origin of urea from ammonium carbonate is an interesting practical point, and one worth bearing in mind in the case of a patient receiving this drug medicinally, in examining the urine in disease for excess of urea.

Uric Acid does not, in my experience, occur in the urine of the horse excepting as the result of disease, and practically we may regard uric acid in herbivora as replaced by hippuric acid, though the latter is at once replaced by uric

* Ellenberger's 'Physiologie.'

acid in starvation (when the animal becomes carnivorous) or, as mentioned before, in the young animal still sucking its mother.

Hippuric Acid.—Our knowledge of the seat of formation of this acid in the animal body is due to the experiments of Bunge and Schmiedeberg, and I shall attempt here to embody the authors' views on the subject.*

The carbon of the food which is not rejected by means of the lungs, unites with nitrogen and forms a series of bodies which escape by the kidneys; these bodies are urea, uric acid, hippuric acid, creatin, and creatinin. Hippuric acid is formed in the animal body by the combination of benzoic acid and glycocoll, the latter arising possibly from the decomposition of albuminous tissues, the former being derived from the food through various aromatic combinations contained in plants.

Great doubts having arisen as to where the synthesis of glycocoll and benzoic acid occurred, the authors, by means of experimental inquiry, ascertained that the combination occurred in the kidneys, that it was brought about by the living cells of the kidney, and that the red blood corpuscles took an active part in the process through the oxygen they contain.

They cautiously observe that in dogs only has the exclusive formation in the kidney of hippuric acid been observed, for rabbits can form this acid even when the kidneys are extirpated.

Hippuric acid exists in the urine either as hippurate of lime or potash, probably the former. There are no free acids in the urine, even in carnivora; and in omnivora the same holds good, the acidity of the fluid with them being due to acid salts.

The amount of hippuric acid excreted varies with the diet; it is increased by using meadow-hay and oat-straw, and decreased by using clover, peas, wheat, oats, etc.; as the urea rises the hippuric acid falls.

According to Munk, a horse fed on meadow-hay excreted

* 'Physiological and Pathological Chemistry,' Bunge.

1·76 ozs. of hippuric acid per diem; fed on oats and a moderate amount of hay ½ oz. to ¾ oz. per diem is yielded. This was the mean amount I found in horses fed on the same diet.

Liebig, many years ago, started a theory that benzoic acid was found in the urine of working horses, and hippuric acid in the urine of those at rest; I have endeavoured to find out what truth there was in the statement. My observations showed that hippuric acid is generally found in the urine of working horses, and seldom found in the urine of horses at rest—in fact, the reverse of Liebig's theory. Hippuric acid is rarely to be found in urine 24 hours old; in fifty-four specimens I only found it eight times; this is due to its fermentative decomposition.

Benzoic Acid is the antecedent of hippuric. As just mentioned, it is derived from the benzoic-acid-forming substances in vegetable food. The amount found in the urine of horses at rest is about ¼ oz. per diem.

Sulphuric Acid exists in the urine in two forms: first, as an inorganic compound; second, as ethereal sulphates. Both are derived from the decomposition of proteids, but the ethereal sulphates or sulphonates are combined in the form of a potash salt with phenol, cresol, catechol (or pyrocatechin), indol, and skatol.

These ethereal sulphates occupy an important position in the composition of the urine of herbivora, as they are largely derived from the aromatic substances found in their food, or from the splitting up of the complex albumin molecule during pancreatic digestion. In carnivora and omnivora the ethereal sulphates are a measure of the amount of decomposition occurring not only in the proteids of the body, but of active putrefactive changes occurring either in the intestinal canal or outside it, such as in septic and suppurative diseases. This will not hold good for the herbivora, as much of the material excreted does not arise from putrefaction, but is taken in with the food.

The union of the ethereal sulphates with the aromatic compounds takes place in the liver. When the phenol

sulphate is excreted it undergoes change in the presence of the oxygen of the air, forming, amongst other bodies, pyrocatechin, which gives the brown colour to stale urine. The daily amount of ethereal sulphate compounds is about $\frac{1}{4}$ oz.

Another sulphur compound of the urine is sulphocyanic acid, found regularly in the urine of herbivora. The only other substance of this class to which allusion will be made is indoxyl or indican, which is formed from indol, and yields on oxidation indigo blue, which is commonly found in the urine of the horse.

The **Colouring Matter of the Urine** is urobilin, which is a decomposition product of hæmoglobin; the change may possibly take place in the liver, though it is generally supposed to occur in the small intestine, through the bile pigment being acted upon by the nascent hydrogen, the product being absorbed and excreted by the kidneys. It is generally considered that there is only the one urine pigment; it is certain, however, that in a diseased condition other decomposition products of hæmoglobin appear.

The inorganic substances found in the urine are chlorine, salts of calcium, magnesium, sodium, and potassium, phosphoric, sulphuric, and silicic acids.

The nature and proportion of the salts vary with the diet. Of the alkalies, potassium salts predominate in the urine of the horse; calcium salts are also largely represented. Meade Smith gives the following ash composition of horse's urine:

Potassium - -	36·85 per cent.
Sodium - -	3·71 „
Calcium - -	21·92 „
Magnesium - -	4·41 „
Phosphoric acid.	—
Sulphuric „ -	17·16 „
Chlorine - -	15·36 „
Silicic acid - -	·32 „

The quantities in this ash analysis do not agree with my observations, but they convey the same truths, viz., the

heavy proportion of potassium salts, the small proportion of sodium salts, the excess of lime salts, the small proportion or absence of phosphoric acid, the large proportion of sulphuric acid, and the small amount of magnesia.

There is a considerable variability in the ash analysis, which, no doubt, is largely due to the difference existing in foods. It has been found that in ruminants the calcium salts are mostly excreted with the fæces, whereas in the horse the bulk passes through the kidneys; in the same way it is said that sheep excrete nearly all the potassium of the food by the kidneys, whilst the horse only excretes rather more than half by this channel. It is certain that phosphoric acid, which forms such a prominent feature in the urine of carnivora and omnivora, is in the horse almost wholly excreted by the intestines.

Calcium.—More lime exists in the urine than is soluble in an alkaline fluid, so that we have both suspended and dissolved lime, the former increasing with the age of the urine owing to the development of ammonia, until presently the whole of the lime is precipitated. The lime exists in combination with oxalic, carbonic, hippuric, and sulphuric acids. The whole of these combinations do not necessarily exist in one specimen of urine; the salts formed depend upon the amount of lime and the affinity it possesses for the unsaturated acids. I cannot find that the amount of lime in the food influences the production through the kidneys, but I have found more lime in the urine of horses at work than of those at rest. Oxalate of lime crystals are common microscopic deposits in the urine of the horse; the oxalic acid is probably in part derived from the food.

Magnesium in the urine is also suspended and dissolved, the amount which is suspended being increased by that thrown down by the ammonia generated as the urine gets older.

Potassium exists largely in the urine, derived from the potash of the food; it forms numerous combinations, the one with carbonic acid being the cause of the fixed alkalinity of the urine. There is more potash found in the

urine of horses at rest than of those at work, which is explained by the considerable amount of potassium excreted with the sweat.

Sodium only exists in the urine in small quantities, which is due to the fact that very little sodium is found in vegetable food. In the chapter on 'The Constituents of the Organism' the question of sodium in the feeding of herbivora is discussed (p. 19).

The **Sulphuric Acid** in its organic combination has been dealt with previously. The inorganic sulphur is combined with the alkalies; work does not influence its production; about $\frac{1}{4}$ oz. is excreted daily. The origin of the urinary sulphates is from the decomposition of the proteids of the tissues.

Chlorine is supplied by the chlorides of the food. The proportion of chlorine in the food of herbivora is not very high; the amount secreted by horses is between $\frac{3}{4}$ ozs. to 1 oz. per diem, and this, united to the small amount of sodium present, equals a daily excretion of $85\frac{1}{4}$ grains of common salt.

Phosphoric Acid, though existing largely in food, such as oats, passes off almost wholly by the alimentary canal. Sometimes only traces are to be found in the urine; at others the amount is marked, but never considerable. Work does not influence its production.

Ammonia.—I believe that free ammonia exists in the urine of herbivora. It may be that, owing to the amount of mucin, the urine has undergone ammoniacal fermentation in the bladder; but it is certain that perfectly fresh urine gives marked evidence of the presence of free ammonia. On standing a short time, especially in summer weather, the urea decomposes and carbonate of ammonia is largely formed.

The following table, published in my paper on 'The Urine of the Horse,' gives the mean composition of this fluid, which has been compiled from a considerable number of analyses:*

* Proceedings Royal Society, No. 283.

TABLE SHOWING THE MEAN COMPOSITION OF THE TWENTY-FOUR HOURS' URINE OF HORSES AT REST AND WORK.

	Rest.	*Work.*
Quantity	8·689 pints	7·877 pints
Specific gravity	1036	1036
Total solids	8·114 ozs.	8·188 ozs.
Organic solids	5·155 ,,	5·368 ,,
Inorganic solids	2·94 ,,	2·820 ,,
Urea	3·4744 ozs.	
Ammonia carbonate as urea	·4626 ,,	
Ammonia	·887 ,,	·187 ,,
Benzoic acid	·23 ,,	
Hippuric acid		·549 ,,
Phosphoric anhydride	·046 ,,	·067 ,,
Sulphuric ,,	·375 ,,	·539 ,,
Other sulphur compounds	·258 ,,	·271 ,,
Chlorine	1·118 ,,	·775 ,,
Calcium oxide	·121 ,,	·067 ,,
Magnesium oxide	·105 ,,	·093 ,,
Potassium ,,	1·290 ,,	·954 ,,
Sodium ,,	·088 ,,	·064 ,,

The following summary of the urines of animals other than the horse is from Tereg.*

The Urine of the Ox is much the same as the horse, excepting that it is secreted in larger amounts, 21 to 28 pints, more or less, the differences largely depending upon the amount of nitrogenous matter in the diet, for it has been shown that the more nitrogen a diet contains the larger the amount of water consumed.

The fluid is clear, yellowish, and of an aromatic odour; it is of a lower specific gravity than the horse, 1020 to 1030 (in milch cows, according to Munk, 1006 to 1015), owing to the larger amount of water secreted, and being poorer in solids.

The nitrogenous matter in the urine, mainly represented by urea and hippuric acid, varies according to the diet. On a diet of wheat straw, clover hay, beans, starch, and oil, the amount of urea was found to be 4·06 per cent.;

* Ellenberger's 'Physiologie,' Art. 'Harn.'

whilst on one of oat straw and beans the urea fell to ·84 per cent. When the urea is high, the hippuric acid is low, and *vice versâ*. The largest amount of hippuric acid is produced by feeding on the straw of cereals, the smallest amounts by feeding on leguminous straw, whilst a medium amount is produced by feeding on hay.

The urine of ruminants contains less aromatic sulphur compounds than that of the horse, and more of the inorganic sulphur, but, like the horse, the phosphates are either absent, or only occur in small amounts.

Here is a table of Tereg's showing the composition of the urine of the ox on different diets, the observations extending over four months:

	lbs.	*lbs.*	*lbs.*	*lbs.*
Total quantity of urine	26·026	31·174	29·986	18·326
„ „ dry matter	1·716	1·518	1·408	1·144
„ „ ash	·880	1·012	1·034	·660

Calves still sucking excrete an acid urine, rich in phosphates, uric acid, creatinin, and a peculiar substance allantoin; it is poor in urea, and, according to Moeller, contains hardly 1 per cent. of solids.

The Urine of the Sheep has an alkaline reaction, and the amount excreted is from ·85 pint to 1·36 pints. Tereg gives the following percentage composition of a sample:

Specific gravity	1072
Water	86·48
Organic matter	7·96
Inorganic matter	5·56

The organic matter contained:		*The inorganic matter contained:*	
Urea	2·21	Chlorine	1·05
Hippuric acid	3·24	Potassium choride	1·84
Ammonia	·02	Potassium	2·08
Other organic substances	2·07	Lime	·07
Carbonic acid	·42	Magnesia	·20
		Phosphoric acid	·01
	7·96	Sulphuric „	·24
		Silica	·07
			5·56

In sheep urea and hippuric acid stand in the proportion of 2 to 3, whereas in cattle on the same diet the proportion is 16 or 20 of urea to 11 or 13 of hippuric acid.

It is strange that the food most productive of hippuric acid in the horse is the least productive of this substance in the sheep. Old meadow hay produces a large quantity of hippuric acid in the horse, whilst *new* meadow hay has this effect on sheep.

In sheep there is three times more magnesia than lime in the urine, whereas the reverse is the case in the fæces of the same animal.

The **urine of the pig** resembles that of carnivora, but its composition, etc., depends on the character of the food. The specific gravity is 1010 to 1015, it is either acid or alkaline, and contains uric acid, xanthin, guanin, and much urea.

Secretion of Urine.—The physiology of the secretion of urine was touched on at the early part of this chapter (p. 197); it is a comparatively simple process, and consists in the difference in pressure between the blood in the Malpighian bodies and the tubules; in this it differs markedly from the saliva, gastric juice, and bile (Landois and Stirling). When the pressure in the tubules amounts to two-thirds of the pressure in the renal arteries, the secretion of urine ceases.

This theory of urinary secretion has been termed the filtration theory, but there are certain facts which tend to show that such a view of the matter is incomplete, and that it is necessary to take into consideration the vital activity of the cells lining the tubules. Blood pressure doubtless plays an important part in the process, but it will not account for an acid urine, nor the presence of a large quantity of such substances as urea, hippuric acid, creatine, etc., which are either absent from the blood or only found in it in traces, and these are beyond doubt excreted by the epithelial cells of the tubules.

We have before drawn attention to the parts of the kidney in which the various constituents are excreted.

The waste products, viz., the organic and inorganic matters, are doubtless excreted in the tubules, the water in the Malpighian tufts, and if Ludwig's idea is correct of a partial reabsorption of water after leaving Bowman's capsule of the tuft, then it appears probable that the remarkable constrictions in the tubules are for this purpose.

The peculiar elective power so often shown in the tissues of the body is nowhere better demonstrated than in the kidney. After the water has been removed from the blood in the Malpighian tuft, the efferent vessel forms a plexus around the tubules, and from the same blood which has had the water removed, we now have the waste products and inorganic matter separated.

The urine is always being excreted, and falls drop by drop into the bladder, the ureters penetrating the coats of the latter obliquely, so that as the organ becomes distended pressure is exercised on these openings, and no reflux can occur.

Micturition.—In the lumbar portion of the spinal cord is situated the centre for micturition; it is by afferent and efferent nerves in direct communication with the bladder. Through it the sphincter of the bladder is controlled reflexly, tightening its grip consciously and unconsciously on the neck of the bladder as the fluid within increases in quantity, and by means of this centre the mind is made aware of the distension which exists. The desire for micturition having become pressing, the sphincter through the same channel is relaxed as a voluntary act, the diaphragm is fixed, the abdominal muscles and involuntary muscle of the bladder wall contract, the urine is forced into the urethra, where it is hurried along by the accelerator urinæ muscle. During the act both the horse and mare stand with the hind-legs extended and apart, resting on the toes of both hind-feet, thereby sinking the posterior part of the body: the penis or vulva is protruded, the tail raised and quivering. The stream which flows from the two sexes is very different in size, depending on the relative diameters of the urethral canal. The urethra, excepting

when urine is flowing along it, is a *closed* channel, the walls of which are in apposition. The mare after urinating spasmodically erects the clitoris, the use of which it is difficult to see; it may be due to the passage of a hot alkaline fluid over a remarkably sensitive surface.

The horse can under ordinary circumstances only pass his urine when standing still, though he can defæcate while trotting; but a mare, if considerably excited, can empty the bladder even at a canter.

In the ox, owing to the curves in the urethral canal, the urine simply dribbles away, being directed towards the ground by the tuft of hair found on the extremity of the sheath. The ox can pass his urine while walking.

The cow sinks her body to urinate, but instead of extending her hind-limbs as does the mare, she brings them under the body, at the same time raising her tail.

The centre for the renal nerves is said to be in the floor of the fourth ventricle, puncture of which part produces diabetes.

The nerves supplying the neck of the bladder originate in the sacral region, and injury to the part produces paralysis of the neck and constant dribbling of urine. Severe injury to the spinal cord may exist far forward without any immediate sign of bladder trouble being present; in such cases the work is carried on by the centre in the lumbar cord.

Abnormal Constituents and Urine-testing.

Although I have made it a rule throughout this work to avoid the introduction of methods of inquiry, for the reasons stated in the preface, yet I feel compelled to depart from this course in the present instance, as the question of the composition of the urine in health and disease has a most important clinical aspect. I shall here mention the abnormal substances found, and afterwards deal generally with urine-testing.

Albumin.—At least two forms of albumin may exist in the urine, viz., serum albumin and serum globulin, and to

these we may add a third, albumoses. If urine containing globulin be *saturated* by prolonged shaking with crystalline magnesium sulphate, a precipitate is produced which is serum globulin; the precipitate is best obtained with a faintly acid urine. This test, however, applied to the urine of the horse is liable to fallacy, for the reason that there are certain other substances of a normal kind precipitable by saturation with $MgSO_4$; the process, therefore, can only be employed where albumin is proved by other tests to be present, and when we are capable of recognising by sight the difference in the physical character of a $MgSO_4$ albuminous precipitate and a non-albuminous one. Assuming a proteid is thrown down by $MgSO_4$ the fluid is filtered, and is then saturated by crystalline ammonium sulphate; this throws down serum albumin and albumoses, the former in flocculent masses. By these tests we are capable of distinguishing the *nature* of the proteid excreted; by the following tests the *presence* of albumin only is indicated:

(1) Take the reaction of the urine: if acid add a drop or two of nitric acid and boil—a precipitate appears; if the urine be alkaline rather more acid will be required, but an excess must be avoided, or acid albumin will be formed which is not precipitable in an acid fluid on boiling. (2) Boil the urine; phosphatic turbidity may occur, or proteid, if present, be precipitated. Add a drop of acid, the phosphates or carbonates are at once cleared up, whilst the proteid is unaffected. This test is an important clinical one.

When a urine to which nitric acid has given a turbidity clears up on boiling and becomes turbid on cooling, albumoses—a peculiar variety of proteid—are present. These appear to be common in the horse.

The proportion of albumin present in a urine is roughly judged of by the height of the precipitate in the test-tube after standing from 12 to 24 hours; thus we speak of $\frac{1}{3}$ or $\frac{1}{4}$ albumin; for clinical purposes this is often sufficiently accurate.

There are many other tests for proteid in urine, but

those mentioned are generally at hand and readily applied.

Albuminuria is a rare disease amongst horses as the result of kidney affection, but common enough in many febrile states of the system; for instance, in pneumonia it is exceedingly common, and its presence or absence a valuable guide in forming an opinion of the case.

Sugar in the urine is distinctly rare, though other substances may be present which give a sugar reaction and yet are not sugar.

Sugar is detected by adding to urine a few drops of a weak solution of copper sulphate and an excess of caustic potash; the fluid is boiled, and if sugar be present the whole is turned yellow or red, and throws down a brick-red deposit of the suboxide of copper.

The only error which can be made in this test is taking for suboxide of copper the precipitate which always forms in urine when boiled with copper and potash; the precipitate is *brown*, and the fluid is not turned yellow or red.

Substances may be present in urine other than sugar which reduce copper. When this is suspected, the only reliable clinical test is the fermentation one: yeast is mixed with the urine in a test-tube inverted over mercury, and if sugar be present it undergoes fermentation, CO_2 is given off and collects in the tube.

Bile.—In many cases of liver disease it is important to know whether any of the bile pigments or bile acids are passing out with the urine. For this purpose a drop or two of the urine is placed on a white plate and touched with a rod dipped in strong common nitric acid; a play of colours occurs—green, blue, violet, red, and orange. This test, known as Gmelin's, is characteristic of the bile pigments. (See p. 161.)

The bile acids are recognised in urine by what is known as Pettenkoffer's test. To the urine in a test-tube is added a strong solution of cane-sugar, followed by a few drops of strong sulphuric acid; a purple colour is indicative of the presence of glycocholate and taurocholate of soda.

Mucus in large quantities is a normal constituent of horse's urine, but under disease the amount may be so increased as to render the urine more like linseed-oil. This might be taken for albumin. To distinguish it as mucin, it presents none of the albumin reactions mentioned, and is not affected by boiling. Acetic acid gives a precipitate or cloudiness with mucin, *insoluble in excess.*

Pus is rarely present in urine, due to the fact that suppurative disease of the kidneys or bladder in animals is certainly uncommon. Pus is distinguished by its microscopical appearance; the urine likewise gives an albuminous reaction.

Blood.—The only reliable clinical test is the microscope. The presence of blood can with certainty be determined by the spectroscope. The coffee-coloured urine of azoturia is due to methæmoglobin.

Carbolic Acid is found in the urine of horses combined with sulphuric acid. It can readily be detected by distilling urine with sulphuric acid; the distillate smells strongly of the acid. It is a normal constituent, but is said to be absent in bowel affections, though this does not accord with my experience, so far as I have had an opportunity of observing.

A rough but useful clinical examination of the urine may be made in the following way:

Take the **Reaction** of the fluid with test-paper; it is always markedly alkaline in health, and almost invariably acid in inflammatory diseases.

The **Specific Gravity** may be taken by an ordinary urinometer, using it at the temperature at which the instrument is graduated, generally 60 Fahr.

The **Colour** is judged of by transmitted light, some filtered urine being placed for this purpose in a test-tube and held up to the light. Occasionally the urine gives one colour by reflected, and another by transmitted light; the reflected light is often blue. This is generally, perhaps always, found in stale urine or urine 24 hours old. I have never seen it in the perfectly fresh fluid; it is due to indigo blue.

The colour of healthy filtered urine is yellowish-red or yellow; but a great deal depends on its age. It always turns brown on standing a few hours, the brown colour

Fig. 12.—Crystals of Nitrate of Urea (Funke).*

commencing on its surface and extending downwards, due to the oxidation of pyrocatechin. This substance reduces salts of copper (see *Sugar*).

Urea, if in excess, may be precipitated by strong nitric

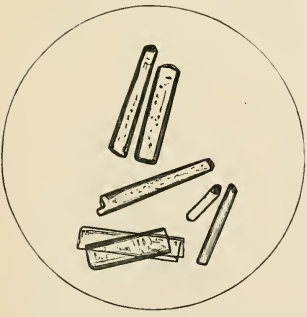


Fig. 13.—Crystals of Impure Hippuric Acid.

Fig. 14.—Crystals of Purified Hippuric Acid (Funke).

acid. If the normal bulk of urine is being excreted, urea is not precipitated until after gently evaporating the urine to

* 'Atlas of Pathological Chemistry.' Supplement to Lehmann's Physiological Chemistry' (Cavendish Society).

half its bulk, and then adding the acid. The crystals should be examined microscopically to prove their nature, as hippuric acid may be thrown down (Fig. 12). Should albumin be present in the urine, it must be removed before carrying out the urea test.

Hippuric Acid is precipitated by evaporating the urine to half its bulk with milk of lime, and adding HCl in excess; either at once or in the course of a few hours dark sea-weed-like masses of impure crystals are obtained (Figs. 13 and 14).

Benzoic Acid is obtained by the same method as hippuric. The deposit is much more granular and occurs immediately on the addition of the acid; but the microscope should be

Fig. 15.—Crystals of Benzoic Acid.

used to determine between them, hippuric acid being in long needles, benzoic in irregular leaf-like plates (Fig. 15).

Uric Acid, if present (abnormal), is precipitated by evaporating the urine to small bulk and adding HCl. The crystals may be identified by the microscope (Fig. 16), or by evaporating them to dryness by means of gentle heat with nitric acid on a white surface, and touching them with dilute ammonia, a beautiful purplish-red colour is developed. This is known as the murexide test.

Indigo is readily precipitated in a white basin by the HCl method. On standing a few hours the vessel has well-marked films of blue on it.

Chlorides are detected by acidulating the urine with dilute nitric acid, and adding a few drops of silver nitrate; the white curdy precipitate is completely soluble in strong ammonia, but insoluble in nitric acid. This test should be

FIG. 16.—CRYSTALS OF URIC ACID (FUNKE).

regularly used in cases of pneumonia, where a decrease in chlorides occurs which persists until death; the return of chlorides generally means recovery. It is obvious that the

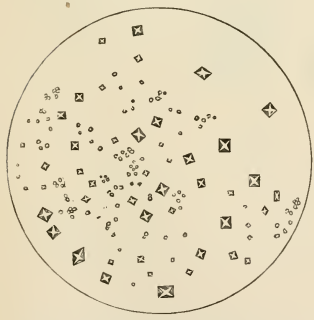


FIG. 17.—CRYSTALS OF OXALATE OF LIME (FUNKE).

FIG. 18.—CRYSTALS OF CARBONATE OF LIME (FUNKE).

same bulk of urine should always be acted upon, as it is simply by judging the depth of the precipitate that we can surmise an increase or decrease in the chlorides, and

even this is liable to fallacy from concentration or otherwise of the urine, or from the administration of chlorides to the patient.

Lime is precipitated by the addition of ammonium oxalate. The fluid should stand some hours to allow the white precipitate to settle. A considerable quantity exists in the urine of herbivora in combination with oxalic and carbonic acids (Figs. 17 and 18).

Magnesium.—To the fluid from which the lime has been removed by filtration add phosphate of soda and ammonia; allow to stand some hours; magnesium settles. Very large crystals may be produced by this process (Fig. 19).

Sulphuric Acid.—A white precipitate, formed on the addition of barium chloride, insoluble in nitric acid. Before

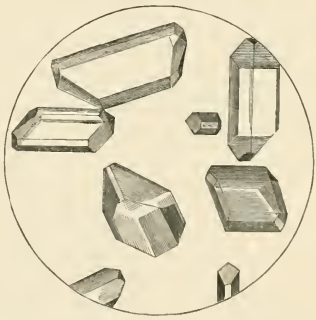


Fig. 19.—Crystals of Triple Phosphate (Funke).

adding the barium the fluid should be acidulated with hydrochloric acid; but the latter must be pure and free from sulphuric acid.

Phosphoric Acid.—Found only in small quantities in healthy, but largely in acid urine. Phosphates produce a turbidity on heating the urine, removed by the addition of a drop of nitric acid. They produce a precipitate with silver nitrate, *soluble* in nitric acid.

Soda and **Potash** cannot be roughly determined, as they

require a tedious isolation which can only be carried out in a laboratory.

For all the above observations filtered urine should be used.

To obtain deposits for microscopical examination, the unfiltered urine is placed in a glass and allowed to stand for some hours; the deposit may be taken up with a pipette and placed on a slide.

In this way red blood corpuscles, pus, casts, epithelium, etc., may be readily determined. The inorganic deposits of healthy urine are carbonate of lime in beautiful large wheel-shaped, dumb-bell, or rosette crystals (Fig. 18), and oxalate of lime (Fig. 17), in unmistakable octohedra or square envelope-shaped crystals, insoluble in acetic acid, carbonate of lime being soluble. Occasionally considerable quantities of oxalate crystals are formed; they are nearly always very small in size, though sometimes large. If the urine be very alkaline from standing, quantities of the large tombstone or coffin lid crystals of ammonio-magnesium phosphate are found; they can be readily seen by the naked eye as glistening glass-like masses (Fig. 19).

Such are the common crystals found in normal urine.

CHAPTER XII.

NUTRITION.

Income and Expenditure.—A constant and fairly regular waste is daily occurring in the bodies of animals, due to the internal work of the system, the production of heat, and, if labour be performed, to muscular movement. It is, therefore, best to describe the work of the body as of two kinds: viz., internal work, such as the movement of the heart, lungs, bowels, and the production of animal heat; and external work, due to muscular movement.

If the food an animal receives is neither greater nor less than its requirements, the body-weight remains unaltered; if, on the other hand, the food is deficient in amount the body loses weight, whereas if in excess it gains weight. By physiological equilibrium we understand that the income is equal to the expenditure, and the body-weight remains unchanged.

It is necessary, however, that the food an animal receives should supply the various tissues of which the body is composed, for it is quite possible to conceive a food which, though equalling in weight a diet which has produced physiological equilibrium, is yet one on which a loss of body-weight is occurring, for the reason that it is deficient in some of the elements out of which the tissues are repaired.

The animal body consists of proteids, fats, salts, water, and a very small proportion of carbo-hydrates. Every food must either contain these principles, or must be capable of conversion into them after having entered the body. According to Bischoff, the animal body consists of—

Water	-	64 per cent.
Proteids	-	16 „
Fat	-	14 „
Salts	-	5 „
Carbo-hydrates	-	1 „

The water being in the largest, and, excluding the carbo-hydrates, the salts being in the smallest, proportion. If the body of an animal be examined, it is found that the largest portion of it is muscular tissue—in the horse 45 per cent. at least.

The following table is from Tereg's article on the 'Exchange of Material.'*

	Ox. *Half fattened.*	*Sheep.*	*Pig. Fat.*
	For 500 parts of body weight.	For 50 parts of body weight.	For 75 parts of body weight.
Water	257·5	25·1	31·0
Dry substance	201·5	20·3	41·0
Contents of intestines	41·0	4·6	3·0
	500·0	50·0	75·0
Composition of the dry substance:			
Proteids	83·0	7·00	8·2
Fat	95·5	11·75	31·6
Ash	23·0	1·55	1·2
	201·5	20·30	41·1
Elementary composition of the organic substance:			
Carbon	116·97	12·71	28·52
Hydrogen	17·20	1·89	4·28
Oxygen	30·20	2·96	5·60
Nitrogen	13·30	1·12	1·32
Sulphur	·83	·07	·08
Composition of the ash:			
Phosphoric acid	9·150	·605	·477
Lime	10·500	·682	·465
Magnesia	·423	·0262	·0234
Potassium	1·020	·085	·101
Sodium	·727	·052	·0534
Iron	·199	·0211	·0098
Sulphuric acid	·189	·0177	·0212
Carbonic acid	·434	·0267	·0154
Chlorine	·294	·0257	·0314
Silicic acid	·064	·0101	·0022

* Ellenberger's 'Physiologie.'

We can readily understand why it is that the food taken into the body should contain the same principles as the organism.

These principles are constantly undergoing change, the nitrogen being oxidized into urea and other products of nitrogenous metabolism, and the fats into carbonic acid and water.

The **Income** of the body is the food taken into the digestive canal, and the oxygen taken in at the lungs.

The **Expenditure** consists of the **Carbon** in the form of carbonic acid expired at the lungs, the small and unknown quantities given off by the skin, and the carbon excreted by the urine; the **Nitrogen** excreted in the form of urea, hippuric acid, and other substances given off by the kidneys; the **Inorganic Salts** excreted by the kidneys, through the skin, and mixed up with the various digestive secretions; the **Water** given off at the lungs by transpiration, through the skin, by the kidneys, and an amount got rid of by ordinary secretions.

Besides these we have the excretion of fæces, containing those portions of the food which the system has been unable to assimilate, and mixed up with them are certain of the secretions found in the intestine. The fæces do not constitute an expenditure, though, in ascertaining what the system has assimilated, it is clear that they must be deducted from the food ingested.

There are other sources of loss besides those mentioned above, such as the production of milk, wool, and semen; but as these have only special application, the general statement made above is not affected.

The material supplying the income of the body consists of so much carbon, hydrogen, oxygen, nitrogen, sulphur, and phosphorus; and the matter forming the expenditure also consists of the same elements. When the body is in a state of equilibrium, the amount of these elements excreted is the same as the amount ingested, and this is the principle on which all observations on the wear and tear of the body

have been made. The composition of everything passing into the body and the exact composition of everything passing out of it is a tedious experiment to make, and one liable to considerable error.

Boussingault many years ago made income and expenditure experiments on all domesticated animals, and recently a most elaborate balance-sheet has been drawn up for the horse from the experiments of Zuntz and Lehmann.* I have reproduced this table, converting the weights into pounds and ounces; this latter has occasioned a slight discrepancy, inasmuch as the elements expended do not agree exactly with those taken in. The error, however, is trivial, and the table is introduced as an example of how observations of this kind are made. The first portion of it illustrates also the method by which digestion experiments are carried out. As the horse on which this experiment was carried out neither lost nor gained weight, and was kept at rest, it is evident that the income balanced the expenditure, so that the quantities representing the income are the amounts of the elements required by this horse for 24 hours.

In looking at income and expenditure tables of a body in perfect equilibrium, it is necessary to remember that, though the amount of the elements going out correspond to the amount taken in, the elements passing away are not immediately derived from those which have passed in; everything passing out must have been of tissue origin, and have formed part and parcel of the tissues. To make the matter clearer, take the nitrogen in the table—viz., nearly 3 ozs. per diem—excreted by the kidneys: it does not follow that this nitrogen was derived from the 18 ozs. of proteid entering the system, but it was derived from 18 ozs. of living proteid which formed part of the body.

* 'Landwirthschaftliche Jahrbücher,' Band xviii., 1889, Heft 1.

Horse.

COMPOSITION OF THE TWENTY-FOUR HOURS' DIET.

Food in Natural State.	Food free from Water.	Proteids.	Fat.	Carbo-Hydrates.	Cellulose.	Ash.
	lbs.	ozs.	ozs.	ozs.	ozs.	ozs.
Oats - -	10·909	9·292	17·458	9·829	98·837	17·370	5·219
Hay - -	6·612	5·271	9·417	3·851	37·975	24·812	8·422
Straw - -	6·306	2·794	·709	1·174	14·615	24·865	3·181
Total - -	23·827	17·357	27·584	14·854	151·427	67·047	16·822
Amount unconsumed -		·357	·638	·257	2·581	1·671	·560
Amount consumed -		17·000	26·946	14·597	148·846	65·376	16·262
Fæces - -		8·104	8·817	6·087	45·985	56·326	12·471
Amount digested -		8·896	18·129	8·510	102·861	9·050	3·791

The lungs absorbed 10·550 lbs. of oxygen.

The elementary composition of the above diet was:

INCOME.

Total amount of food required to support the body for twenty-four hours.	Carbon.	Hydrogen.	Oxygen.	Nitrogen.	Sulphur.
ozs.	ozs.	ozs.	ozs.	ozs.	ozs.
Proteids - - 18·100					
Fat - - 8·528	65·872	9·190	229·286	2·895	·180
Carbo-hydrates - 111·950					
Atmospheric oxygen - 168·844					

The urine contained 2·896 ozs. of nitrogen, and 6·179 ozs. of carbon.

EXPENDITURE.

		Carbon.	Hydrogen.	Oxygen.	Nitrogen.	Sulphur.
ozs.		ozs.	ozs.	ozs.	ozs.	ozs.
·4521	Sulphuric acid - -			·271		·180
13·536	Urinary organic matter -	6·179	·655	3·806	2·896	
·564	Marsh gas - -	·423	·141			
75·551	Water - - -		8·394	67·156		
217·321	Carbonic acid -	59·269		158·052		
	Total - -	65·871	9·190	229·285	2·896	·180

In the preceding table the channels whereby loss occurred to the system were the lungs, urine, skin, etc.; but where animals are yielding milk, wool, etc, these have also to be taken into consideration, the milk especially causing a considerable body drain.

In the following table by Henneberg, quoted by Tereg,* we have a balance-sheet furnished for an ox fed for beef. The food supply is here in excess of the requirements, and, in consequence, material is stored up in the system.

Henneberg fed a full-grown ox, weight 1570·35 lbs, for 28 days with 11·02 lbs. of clover-hay, 13·224 lbs. of oat-straw, 8·154 lbs. of crushed beans, ·132 lb. of salt, and 123·644 lbs. of water. During the experiment the animal increased daily 2·280 lbs. in weight.

The following table shows the income and expenditure occurring in the body during the above observation. The author offers no explanation of the discrepancy occurring in the income and expenditure of hydrogen and oxygen:

Ox.

INCOME.

	Water.	Mineral matter.	C.	H.	N.	O.
	lbs.	lbs.	lbs.	lbs.	lbs.	lbs.
Respiration, food and water	128·272	1·961	12·838	16·530	·683	10·799

EXPENDITURE.

lbs.		Water.	Mineral matter.	C.	H.	N.	O.
		lbs.	lbs.	lbs.	lbs.	lbs.	lbs.
89·632	Fæces	77·305	1·267	5·697	·683	·231	4·408
30·635	Urine	28·817	·672	·484	·055	·374	·231
21·559	Carbonic acid	...	...	5·884	...	...	15·675
·066	Marsh gas	...	...	·044	·022	...	...
20·943	Water by the lungs and skin	20·943	...	...	...	...	...
	Total	127·065	1·939	12·109	·760	·605	20·314
	Difference	1·207	·030	·729	·110(?)	·078	1·873(?)

The difference represents the amount of material stored up daily in the body of this animal.

* Ellenberger's 'Physiologie.'

These latter figures corresponded to a daily increase of:

	lbs.
Albumin	·484
Fat	·617
Salts	·022
Water	1·157

Metabolism.—By this term is understood the changes occurring in living tissues.

It is evident, from all that has been said, that constant breaking down and building up is occurring in the body: every muscular contraction, every respiration, the beating of the heart, the movements of the bowels, all mean wear and tear, and as rapidly as a part is destroyed it must be replaced. The processes of construction and destruction are known as **anabolism** and **katabolism**; in a perfect state of health they should be in equilibrium. Both are dependent upon definite chemical changes occurring in the system, some of which we have a fair knowledge of; others are wrapped in obscurity.

We have followed the constructive processes from the mouth until the elements of the food pass into the tissues; we have no knowledge of what there endows them with life. We have traced the products of katabolism from the tissues to the lungs and kidneys, and in a future chapter will state what is known of the immediate processes in the muscular tissue, whereby the living substance becomes destroyed, and is cast off from the body through the excretory channels previously dealt with.

Of the total amount of carbon which enters the body with the food, by far the largest quantity is excreted by the lungs; a certain though small proportion is given off from the skin, and in animals which sweat, as the horse, the amount passing off during work may not be inconsiderable; the remainder of the carbon is got rid of in the form of urea, hippuric or benzoic acids, and minor carbon compounds.

The hydrogen of the body is excreted as water, the oxygen as carbonic acid and water, only a small proportion of it being returned in the lowest form of oxidation, viz., urea.

The nitrogen is almost wholly excreted by the kidneys; a small portion may possibly be got rid of by the lungs, and in working horses by the skin. It is usual to regard the urine nitrogen as a measure of the proteid changes in the system, and this nitrogen is got rid of in the form of urea, hippuric acid, colouring matter, and probably ammonia.

The sulphur of the body is got rid of through the kidneys, and by means of the cast-off epithelium, hair, and horn.

It is now necessary to glance at the form in which the various elements of the body enter it, and we will deal first with proteids.

Nitrogenous Food.—If an animal be fed exclusively on a proteid diet, it is found that, practically, the more it gets the more nitrogen is excreted by the kidneys, until at length a stage arrives when the amount of proteid excreted equals the amount taken in; this condition does not last long, and the term applied to it is 'nitrogenous equilibrium.' These experiments have been made on dogs, and it has been observed that in order to produce this nitrogenous equilibrium, a considerable quantity of flesh has had to be ingested, the result being that the animal has gained weight. It is evident, therefore, that if the amount of nitrogen passing out of the body is equal to the amount passing in, and yet, in spite of this fact, the animal is gaining weight, a something in proteid food which is not nitrogen is being stored up; this something is the carbon portion of the proteid substance, and it is found that this is stored up in the body in the form of fat. From these observations it has been determined that a proteid breaks up in the body into two portions: one, the nitrogenous portion, which is excreted as urea; the other, the non-nitrogenous portion, which is stored up in the system as fat.

Under ordinary circumstances the whole of the nitrogen of the proteid is not excreted as urea; a portion remains in the system and is converted into tissue. According to some observers the nitrogenous portion which gives rise to urea has been termed 'the circulating albumin,' the other or smaller portion 'the tissue albumin.'

Considerable discussion has occurred with reference to this theory of Voit's of circulating and tissue albumin, and it is generally considered that the line drawn by this able observer between the two does not hold good, and that he is not warranted in stating that urea is derived from that portion of the proteid which never becomes a part of the living body, and which he terms 'circulating albumin.' That under ordinary circumstances a portion of the nitrogen taken in does form urea and allied substances, whilst another portion is stored up in the tissues, is undoubted; but it by no means follows from this that the urea moiety is not derived from living tissue—in fact, the total weight of evidence is against Voit, for, as Burdon Sanderson expresses it, the production of urea and other nitrogenous metabolites is exclusively a function of living material.

So long, therefore, as we are careful not to regard the circulating albumin as so much dead substance, no harm can arise from the use of the terms 'circulating' and 'tissue albumin,' as expressing the idea that part of the proteid is retained in the body and part cast off from it.

All true proteids are equally capable of becoming part of the tissues when taken as food; but when albuminoids, such, for instance, as gelatin, are consumed, they produce the same amount of urea as an assimilable proteid, but the animal loses flesh, viz., none of the material is stored up in the system.

Non-nitrogenous Food.—When animals are fed on an exclusively fat or starch diet they soon succumb. It is impossible to maintain life on a nitrogen-free diet. In experiments made with fat and starch some proteid must therefore always be given at the same time.

The most remarkable effect of proteid and fat being given together, is the sparing destruction of the proteid; much less is used in the system when fats are given than without them: this is spoken of as the proteid-sparing action of fats. The amount of albumin required by the system is also diminished by the presence of carbo-hydrates; this is an important feature in the feeding of herbivora, in the

food of which very little fat exists. It has been suggested that the proteid-sparing action of carbo-hydrates and fats is due to the fact that they are oxidized more readily than albumin, and that they thus prevent the action of oxygen on this body.

The formation of fat occurs in three ways: (1) From the fat which enters the body, which in the herbivora is small; (2) from the carbonaceous residue of the proteid substances; (3) from the carbo-hydrates of the food. It has been clearly shown by experiment that animals have stored up fat on a purely proteid diet, and, no doubt, the vast quantities of fat found in highly-fed animals, have their origin in the proteid and carbo-hydrate substances of the food.

Owing to the large amount of carbo-hydrate food used by herbivora, and to the fact that carbo-hydrates require less oxygen for their oxidation than fat, more of the oxygen consumed finds its way back in the CO_2 of the egesta with herbivora than is the case with carnivora, where the greater portion of the oxygen leaves the body combined with hydrogen in the form of water. Herbivora therefore use less oxygen than carnivora, and the respiratory quotient, as seen in the chapter on 'Respiration,' is consequently greater.

Inorganic Food.—The changes occurring in the inorganic substances of the body are extremely interesting. It is evident that the daily quantity of salts required must depend upon the age of the animal; young growing animals requiring more than adults.

The remarkable thing about Boussingault's nutrition-tables is, that his animals gave out more salts than they took in with the food. This can only be explained by supposing that the system has the power of storing up inorganic material for future excretion.

In a special experiment made on a cow to determine the income and expenditure of salts, he found that the animal gave up ·205 oz. more silica than it received in the food, but it stored up phosphoric acid and lime. The largest excretion of salts was in the urine, the smallest in the milk,

and the amount of salts passing away with the fæces and of no use to the system was nearly half that ingested.

The salts in the body perform important functions in connection with secretion and excretion; as Foster expresses it, they 'direct the metabolism of the body.' Their distribution throughout the structure is remarkably regular, sodium and chlorides being found in the blood-serum, potassium and phosphates in the red cells, sulphur in horn, potassium in sweat, phosphates and lime in bones, etc. When a deficiency in salts occurs, the body apparently for some time draws on its own store, and then certain nutritive changes follow. Both organic and inorganic salts are required.

I have drawn attention to the remarkable fact that potassium is largely the salt used by herbivora, and sodium only slightly so (p. 20); and further, that horses can be kept in perfect condition without receiving sodium chloride with their food, that which is naturally in it (and the amount is small) being quite sufficient for the uses of the economy.*

Starvation.—When an animal is starved it lives on its own tissues; in the herbivora the urine becomes acid, hippuric is replaced by uric acid, and the secretion becomes clear. The elimination of nitrogen in the starving animal at first falls rapidly, then gradually, and shortly reaches a fluctuating daily quantity.

During starvation the CO_2 excreted falls in amount, and the oxygen absorbed becomes reduced, though not in proportion to the fall of the CO_2.

If water be given, life is considerably prolonged. Colin records a case (to be mentioned presently) where a horse receiving water lived thirty days without food. The loss in weight by starvation consists of two-thirds water, one-twelfth albumin, and one-fourth fat. It is notorious that herbivora, though they lose less proteid during starvation than carnivora, yet do not withstand starvation so well. Nor need we go so far as a starvation experiment to ascertain this fact: when men and horses are being worked hard, whether

* *Journal of Physiology*, vol. xi., No. 6.

the food given be insufficient or sufficient, the loss in condition amongst the horses sets in early, and is extremely marked for some time before the men show any appreciable muscular waste.

One explanation offered as to the reason why herbivora withstand starvation so badly is that they possess less circulating albumin and less tissue albumin. A full-grown ox during starvation has been known to use up only $2\frac{3}{4}$ lbs. of proteid per diem, whilst, judging from carnivora, at least double this amount should have been destroyed (Meade Smith).

Horses have been known to live without food or water for as long as three weeks; but it is said that if they have suffered 15 days' starvation, the administration of food after this time will not save them.

Colin records an experiment where a horse weighing 892·6 lbs. was starved for 30 days, only being allowed 2·46 pints of water per diem. He was nourished on his own tissues, the daily loss in weight being 5·865 lbs., consisting of:

	ozs.
Carbon	27·771
Hydrogen	4·083
Nitrogen	2·647
Salts	·745

which may be taken as representing the daily waste during starvation.

When this animal died, the body weight was 715 lbs., and it was found that of all the organs the kidneys had suffered the greatest loss, 41·6 per cent. of their weight; next the lungs, 38 per cent.; the stomach and intestines (empty), 35 per cent.; the skeleton, 26 per cent.; skin and hoofs, 21 per cent.; muscles, 19·6 per cent.; heart, 17 8 per cent.; pancreas, 17 per cent.; spleen, 16 per cent.; liver, 12 per cent.; brain and spinal cord, 2·3 per cent.

It is most remarkable that the muscles should have suffered so little. It was found that the amount of fat after 30 days' starvation was actually greater than that found in a healthy control animal of equal weight destroyed

for the purpose of comparison; the case must therefore be regarded as exceptional.

In starvation about 90 to 100 per cent. of the fat disappears, and the muscles lose from 60 to 70 per cent. in weight.

Muscular Exertion.—The chief cause of body-waste is work. There are other and smaller causes, but this is obviously the most important. The performance of muscular work increases the action of the heart, lungs, muscles, skin, etc. Potential energy is converted into heat and work, and this is produced by the oxidation of food into its decomposition products.

The changes in the tissue resulting in heat and motion occur almost entirely, if not exclusively, amongst the non-nitrogenous elements. This has been settled beyond all doubt. It is not the nitrogenous substances, as we might suppose, considering their essential nature, which lead to heat and motion; and the urea of the urine does not consequently represent a measure of the work performed. Heat and motion are exclusively the function of the non-nitrogenous food. This is a curious fact, and apparently plunges us into the difficulty of explaining why an animal cannot live, let alone work, without receiving proteids, and that the heavier the work performed the more proteid required. The explanation is that the absorption of oxygen, without which no oxidation of the non-nitrogenous elements can occur, is dependent on the amount of proteid taken in.

Amount of Food required.—Muntz (quoted by Colin), from his investigations into the food required by the Paris omnibus-horses, came to the conclusion that five-twelfths of the total ration was expended on internal work and repair, and seven-twelfths on muscular work; and he showed that a horse performing 9 to 10 miles per diem required for 1,000 lbs. of body-weight:

	lbs.
Nitrogenous matter	2·83
Fatty matter	·75
Non-nitrogenous extractives	17·00
Cellulose and lignin	6·20

On this diet they neither lost nor made flesh.

From experiments made in Germany by Wolff, the following table of food requirements for every 1,000 lbs. of body-weight was compiled:

Animal.	Total amount of Organic Matter.	Assimilable Matter.				
		Albumin.	Carbo-hydrates.	Fat.	Total.	Albuminoid Ratio.
	lbs.	lbs.	lbs.	lbs.	lbs.	
Horses at light work -	21·0	1·5	9·5	·40	11·40	1 : 7·0
„ moderate work -	22·5	1·8	11·2	·60	13·60	1 : 7·0
„ full work -	25·5	2·8	13·4	·80	17·00	1 : 5·5
Oxen at complete rest in stall	17·5	0 7	8·0	·15	8·85	1 : 12·0
Oxen at moderate work -	24·0	1·6	11·3	·30	13 20	1 : 7·5
„ full work - -	26·0	2·4	13·2	·50	16 10	1 : 6·0
Milch cows - -	24·0	2·5	12·5	·40	15·40	1 : 5·4
Fattening oxen : 1st period	27·0	2·5	15·0	·50	18 00	1 : 6·5
„ „ 2nd „ -	26·0	3·0	14 8	·70	18·50	1 : 5·5
„ „ 3rd „ -	25·0	2·7	14·8	·60	18·10	1 : 6·0
Fattening sheep : 1st period	26·0	3·0	15·2	·50	18·70	1 : 5·5
„ „ 2nd „ -	25·0	3·5	14·4	·60	18 50	1 : 5·4
Sheep fed for wool :						
Stronger breeds -	20·0	1·2	10·3	·20	11·70	1 : 9·0
Finer breeds - -	22·5	1·5	11·4	·25	13·50	1 : 8·0

It will be observed that the quantities given in the above table are of 'assimilable matter.' It is a well-known fact that animals can only obtain from food a certain proportion of its nourishment; neither reducing the quantity given nor adding substances to the food will make them digest more than a certain proportion of each proximate principle; the 17 lbs. of assimilable matter for horses in hard work would probably only be extracted by the administration of 25 lbs. of food. Each food and each proximate principle has a digestive co-efficient of its own; and before we can form any opinion of the amount of nourishment a food is capable of supplying, we must apply to it the digestive co-efficients which have been obtained as the result of direct experimental inquiry.

Digestibility of Food.

From a physiological point of view we understand by the digestibility of food, that a portion of each of the proximate principles it contains is capable of being absorbed. Every food contains albumin or proteid, fat, carbo-hydrates, and salts. Of each of these there is a distinct proportion absorbed, and the remainder rejected and excreted with the fæces. The number which represents the quantity absorbed is spoken of as the digestive co-efficient. In each food there is a distinct co-efficient for each proximate principle. The methods employed by which these results have been obtained, have been to feed animals on food of known composition and analyse the excreta; the difference between the albumin, fat, starch, sugar, cellulose, etc., taken in by the mouth, and that rejected from the body by the fæces, is the measure of the amount digested (see table, p. 224).

The digestibility of a food depends upon its age, growth, mode of preparation, and condition. Well-saved hay, for example, is better digested than hay which has been washed by rain. The admixture of other substances with a food also affects its digestibility; the addition of starch or sugar to a diet of hay and straw, if it exceeds 10 per cent. to 15 per cent. of the dry forage, decreases its digestibility; small quantities of oil aid digestion, large quantities retard it. I have found that the addition of oats to a ration of hay increased the amount of hay digested.

Contrary to expectation, experiments made by the French and Germans have shown that neither crushing oats nor cutting hay increases the proportion assimilated by the system; it is certain that, as a practical matter, both these methods of preparing food for horses are highly appreciated in this country, and I think with good reason. I have been led to regard 9 lbs. of crushed oats as equal to 9½ lbs. to 10 lbs. of uncrushed; these results were not obtained as the result of scientific investigation, but as a matter of observation.

Experiments have shown that the same amount of proximate principles are not digested by all classes of

animal; a sheep, for instance, digests hay better than a horse, and this digestion is not limited, as one might expect, to the cellulose only, but is extended to the other proximate principles, excepting the proteids, of which both animals digested the same amount.

The following table will show the average percentage of each proximate principle digested by animals. The figures are the means of a mixed diet:

	Horse.	*Ox.*	*Cow.*	*Sheep.*
Albuminoids -	69	65	57	57
Fatty matter -	59	64	65	61
Carbo-hydrates -	68	66	70	73
Cellulose and fibre	33	60	61	58

By laborious experiments, the digestive co-efficient of all the principal feeding stuffs has been obtained. The subject cannot here be dealt with further; a full account is given elsewhere.*

It is evident that every food, no matter how well-balanced in its proximate principles, will contain a certain proportion of digestible and indigestible matter; the latter, no doubt, largely depends upon the presence of cellulose and lignin. The herbivora, though adapted to digest these, cannot obtain from their food the full amount of nutriment if either of them be in great excess; but apart from this no food is fully digested: there is a certain proportion of proteid, fat, sugar, and cellulose which the animal cannot extract or assimilate from the total amount given it. This is a point of practical importance.

The digestibility of a food is affected by its **Nutritive Relation**, and this term we must now explain. The nutritive relation of a food is: (1) the proportion which the proteids bear to the fat and carbo-hydrates, minus the cellulose; (2) the proportion of fats to the nitrogenous principles; and (3) the proportion of nitrogenous or proteid principles to the whole of the non-nitrogenous. The first is called the nitrogenous ratio; the second the fatty; the third the complete nutritive ratio. By splitting up food into these

* 'Veterinary Hygiene.'

various ratios, we obtain an insight into the chemical arrangement of its constituents, and as the proportion which these bear to each other considerably influences the digestion of a food, the matter is one of practical importance.

The desirable nitrogenous ratio of a diet depends upon the class of animal, the age, and, in the case of the horse, the work which is expected. In the young and growing animal the proportion of proteids to the carbo-hydrates, minus the indigestible fibre, should be 1 : 2 ; at middle age it should be 1 : 3 ; in the adult, 1 : 5. The calculation is effected by dividing the nitrogenous material into the sum of the starch, sugar, and digestible fibre.

The fatty ratio of a food is obtained by dividing the fat into the quantity representing the nitrogenous portion ; the most favourable fatty ratio should not be more than 1 : 2·2 or less than 1 : 3.

The complete nutritive ratio of a food is obtained by dividing the nitrogenous quantity into the whole of the non-nitrogenous ; the chief object of this ratio is to show the proportion of indigestible fibre existing in a food. The complete nutritive ratio should be about 1 : 8·7 or 1 : 9 ; if it be 1 : 10, 1 : 12, or 1 : 15, it would indicate an undue proportion of cellulose and lignin, and such a diet would be unfit for hard-working horses, though suitable for cattle. For horses performing ordinary work, a ratio of from 1 : 8 to 1 : 8·5 is suitable ; for hard-worked horses, particularly for fast work, 1 : 6 or 1 : 7 is judicious.

In the determination of all these ratios, the salts of the food are not taken into consideration.

It is important to remember that the nutritive value of a food is not absolutely determined by its chemical analysis ; bran, for example, gives an excellent analysis, but its nitrogen is useless for feeding purposes.

CHAPTER XIII.

ANIMAL HEAT.

As the result of the changes occurring in the tissues, heat is developed. It is not necessary that carbon should be oxidized to CO_2 to produce heat, though this is by far the largest source of supply to the system: any change, hydration, tissue decomposition, muscular contraction, the passage of blood through the vessels, the friction produced by one articulatory surface moving on another, all result in the formation of heat.

The chief source of continual heat production in the body is the food supplied, and the amount of heat which different articles of food are capable of yielding has been very carefully ascertained by burning them in an apparatus where the heat given off is absorbed by water, and the increased temperature of the water is the measure of the heat produced. This instrument is termed a calorimeter. The measurement of heat produced in the calorimeter is known as a heat-unit, or calorie, and one heat-unit is equivalent to 2·2 lbs. of water raised 1·8° Fahr.

The following is Frankland's table of heat-units for different substances:

1 gramme (15·432 grains) of		Albumin	yields	4263	heat-units.	
,,	,,	Fat	,,	9069	,,	,,
,,	,,	Starch	,,	3921	,,	,,
,,	,,	Grape-sugar	,,	3277	,,	,,
,,	,,	Cane-sugar	,,	3348	,,	,,
,,	,,	Urea	,,	2205	,,	,,
,,	,,	Hydrogen	,,	3450	,,	,,
,,	,,	Carbon	,,	8100	,,	,,

It is necessary to remember that the amount of heat yielded by a body in a calorimeter may be much greater than the quantity of heat which the same substance will yield when oxidized in the body; particularly is this the case with albumin, which in the system is never fully oxidized, as so much of it—one-third—passes off as urea. The albumin in the above table has been corrected for this loss.

Loss of Heat.—The chief seat of heat production is the muscles; heat is also produced in the liver and other glands. Of the total amount produced, some is lost by radiation and evaporation from the skin, and in other ways.

The amounts may be expressed as follows:

Warming solids and liquids	2 per cent.	7 per cent.	15 per cent.
„ air of lungs	5 „		
Evaporation from lungs, say	8 or 9 per cent.		
„ „ skin		85	„
Radiation from skin			
Conduction (ordinarily)		0	„
			100 per cent.

The bulk of the loss is due to evaporation by the skin, and the heating of the inspired air, food, water and fæces, and only a small and varying proportion is due to radiation.

The amount of heat lost by the skin is therefore considerable. The object of this loss is to regulate the body temperature. When animals are varnished, so as to prevent evaporation, the heat of the body does not accumulate as we might expect; on the other hand, a fall in temperature occurs and death shortly follows, the explanation being that the varnish has proved such a good conductor of heat, that more is passing away from the animal than under normal circumstances. If this rapid conduction of heat be prevented by rolling the animal up in wool, death does not follow.

The hairy covering on animals prevents loss of heat by conduction, hair being a bad conductor. When, however, hair is wet, as in sweating horses, it becomes a conductor of

heat, which is thereby lost from the body. We see here the advantage of clipping working horses in the winter. The effect of clipping on the body temperature has been observed by Siedamgrotzky. He found that the temperature of horses rose after clipping, and fell about the fifth day to normal. This rise in body temperature is remarkable, and is possibly explained by supposing that an increased production of heat was set up by cooling the surface.

The **Amount of Heat** produced in the body is spoken of as so many calories produced per hour per kilogramme (2·2 lbs.) of body weight, and the hour-calorie-kilogramme for animals is given by Colin as 2·1 for the horse; sheep, 2·6; man, 2·3; sparrow, 3·2. The smaller the animal the greater the production of body heat.

The quantity of heat developed by a horse in a day is given by Colin as capable of raising by 1·8° Fahr. 4,550 gallons of water, or it will raise from freezing to boiling point a little more than 44 gallons of water.

The **Regulation of the Body Temperature** is no doubt largely produced by the skin. The respiratory passages also assist, which is the explanation of the panting observed in the dog, in which animal the skin practically does not sweat; and the remark respecting panting will apply to cattle, especially those in show condition: here the increased respiratory movement robs the body of heat by warming a larger volume of air. It is more than probable that heat production may be increased or controlled by impressions from the nervous system; section of the sympathetic in the neck causes a rise in temperature on the same side, and division of the spinal cord causes a fall in temperature; but both a rise and fall may be produced by the action of the nerves on the blood vessels, causing dilatation of them with increased flow of blood into the skin, and consequently greater loss of heat; or constriction of the vessels of the skin, followed by a diminished loss of heat.

A loss of heat is also produced by conversion into vapour of the sweat of an active skin, the secretion of which is

wholly under the nervous system. Therefore, by the action of the vaso-motor nerves on the vessels of the skin, and the secretory nerves governing the sweat-glands, the discharge of heat is regulated. But the nervous system has yet a third effect over animal heat. It is believed that certain centres exist in the central nervous system which are in connection with the muscles, and which by reflex action regulate the metabolism of the tissues, and so increase or decrease the amount of heat produced in the part.

The normal temperature of the body in various animals is as follows:

Horse - -	100° Fahr.
Ox - - -	100° to 101° (Colin).
Sheep - -	103° to 104°.

Slight variations are found to occur in the temperature during the twenty-four hours, which have been attributed to the intake of food. The evening temperature is normally higher than that found in the morning. Siedamgrotzky found the highest temperature to be at six o'clock in the evening, and the lowest at four o'clock in the morning.

The same observer studied the influence of feeding on temperature: he found that the temperature rose ·4° to 1·4° Fahr. after feeding, falling to normal in three to five hours. Drinking a pailful of water at a temperature of 50° Fahr. caused the body temperature to fall ·5° to ·9° Fahr.

Feeding and drinking act antagonistically, so that one balances the other.

Exercise raises the body temperature, but to a very variable extent in different horses. Half an hour's trotting raised the temperature ·7° to 2·7° Fahr. After work the temperature at first falls rapidly, and then slowly. In horses which have sweated profusely the resulting fall in temperature carries it below the normal.*

During diseased processes the temperature may run up

* See Siedamgrotzky's interesting paper, for which I am indebted to a translation which appeared in the *Veterinary Journal*, vol. i., 1875.

considerably; 106° Fahr. is no uncommon temperature in the horse; a post-mortem rise in temperature has also been frequently observed. I once found the thermometer register 109° Fahr. placed between the liver and diaphragm of a horse which died from an affection of the liver.

The **Distribution of Temperature** throughout the body has been made the subject of close observation by Colin. He observed that it was common to find the temperature of the blood in the left heart to be higher than in that of the right. He drew particular attention to the fact that the surface temperature of animals presents considerable differences. He found in a horse with a long winter coat (the thermometer standing at freezing-point) that a difference of 44° Fahr. existed between the temperature of the pasterns and that in the rectum, a difference of 35·1° Fahr. between the knee and the rectum, and 5·4° Fahr. between the temperature of the skin covering the chest and that of the rectum.

As we might naturally expect, Colin found from direct experiment that in extremely cold weather those horses with the longest coat had the warmest skins, the difference being as great as 9° or 10·8° Fahr.

The power of resisting cold depends not only on the condition of the skin and the means for preventing loss of heat, but largely on the aptitude of the organism for producing heat, and this latter depends upon the activity of the digestion, the supply and character of the food ingested, and the intensity of the chemical changes in the system (Colin).

In the utilization of animal heat the expenditure must not exceed the income. The means of regulating the equilibrium of heat, so that no more shall be produced than the food supplies, is through the medium of the nervous system.

CHAPTER XIV.

THE MUSCULAR SYSTEM.

THE actual motive-power in the body, whether it be in the moving of the skeleton, the contraction of the heart, or the transport of the ingesta, is performed by the muscular system. It is one of the largest systems in the body, representing no less than 45 per cent. of the body weight. The movement produced by the muscles of the skeleton, heart, and intestinal canal is very different in nature; the skeletal muscles soon tire, the heart and visceral muscles never tire. We find that muscles exist in two well-marked classes—the striated or striped or voluntary variety, and the unstriated or involuntary; the red muscles represent the voluntary or skeletal muscles, whilst the white represent the involuntary or visceral. There is, however, a remarkable exception to this rule: the muscular fibres of the heart, though quite involuntary, are both red and striped.

Composition.—Muscle when examined chemically is found to consist principally of proteids and salts, in addition to which may be found a small quantity of acid, glycogen, traces of urea, and carbonic acid gas. By suitable precautions a fluid can be obtained from perfectly fresh muscle termed muscle plasma; this undergoes coagulation like blood, and yields a clot termed myosin and a serum termed muscle serum. Muscle plasma is a yellowish neutral or alkaline fluid; after clotting and the formation of the muscle serum, the latter is found to be acid. Myosin is a substance obtained after the death of the muscle; there is every reason to

believe that during the life of the muscle it does not exist as myosin, any more than fibrin exists in living blood as fibrin. The living muscle therefore contains myosinogen, or myosin precursor, bearing the closest resemblance to the fibrin of the blood.

Myosin only differs from the blood fibrin by being soluble in a dilute solution of common salt and dilute hydrochloric acid.

The muscle serum consists of three proteids, two being globulins and one an albumin; it possesses an acid reaction due to the presence of lactic acid, the result of the process of coagulation.

In muscle is also found small quantities of volatile fatty acids, such as acetic and butyric, and an organic acid, lactic, which exists in two forms. The importance of this latter acid in the production of rigor mortis, or muscle coagulation, will be dealt with presently. Carbo-hydrate substances, such as glycogen and sugar, are also found in muscles; their function is the liberation of muscular energy. The muscles of the horse contain a considerable quantity of glycogen even after starvation (see p. 166).

Certain extractives can be obtained from muscular tissue, such as creatin, creatinine, carnin, a variable amount of glycogen and sugar, together with a trace of urea, and small quantities of muscle sugar (inosite), alcohol, and lactic acid.

The salts of muscle are principally those of potassium.

A quantity of carbonic acid gas can be obtained from muscle, together with a small proportion of nitrogen, but no oxygen.

Changes resulting from Contraction.—The changes occurring in muscles are remarkably active; the so-called explosions which result in muscular contraction, use up at every moment the combustible material of the structure, and the products arising from their combustion have to be got rid of at once and repair brought about; but changes are constantly occurring even during the period of muscle rest. Muscle activity is characterized by muscle waste; muscle rest is characterized by a preponderance of the process

of repair. We have to learn, therefore, the nature of the waste and repair occurring in muscles, and the physical and electrical phenomena exhibited by muscular tissue during the period of rest and activity.

The oxygen carried to muscles by the blood is absorbed by them in considerable quantities, and a volume of carbonic acid, in less quantities than corresponds to the oxygen absorbed, is returned to the venous blood. Whether a muscle be at rest or active, it is always absorbing O and giving up CO_2, and, moreover, it is always storing up oxygen. The absolute amount of O stored up and CO_2 produced varies considerably in rest and work, being much greater during the latter than during the former condition.

In an active muscle the bloodvessels are more dilated than in the muscle of rest, and this dilatation corresponds to the increased quantity of blood sent to the part, by which alone the irritability of the muscle, or its power of contraction, is maintained; whatever leads to a smaller quantity of blood being sent to an active muscle, produces partial or complete paralysis of the group or groups of muscles affected. This is well seen in the horse when suffering from embolism of the iliac arteries and may readily be produced in the rabbit by compressing the aorta.

Muscles in a state of activity contain less glycogen and sugar than those in a state of rest, due to the amount utilized during muscular activity. But glycogen is not necessarily the source of the energy, since muscles free from glycogen can work normally. Glycogen is rather a convenient accessory than a necessary factor in the production of energy in a muscle.

Active muscles present an acid reaction due to the formation of sarcolactic acid, while the resting muscle is alkaline.

During muscular activity heat is produced, the blood returning from the muscle having a higher temperature than that which supplies it. The amount of heat evolved

varies with the tension of the muscle: the higher the tension the greater the temperature. This has been pointed out as the probable explanation of the high temperatures registered in cases of tetanus. Colin found that the temperature of the masseter muscle of the horse rose 5° Fahr. through feeding. The more fatigued a muscle becomes the less heat it evolves.

Muscles possess, in common with some other tissues of the body, the phenomenon of **Irritability** or **Excitability**, viz., the power of contracting when irritated; the movement in muscle shows itself by the contraction or shortening which occurs. The normal stimulus to muscle is imparted to it through the nerves, but chemical, mechanical, and electrical stimuli also lead to a contraction even in the absence of nerves, or when applied to a muscle removed from the body.

Through the sensory nerves the brain is made acquainted with the position of the body and the state of the muscles, viz., relaxed or rigid, cramped or fatigued. The amount of ordinary sensibility in muscle is not very great unless it be cramped or inflamed. Under these conditions acute muscular pain may be manifest, as we see in the painful lameness of embolism. The special function, however, of the sensory nerves is communication between the exterior and the brain, keeping the latter acquainted with the condition of the former.

By means of the motor nerves the muscles are supplied with the needful stimulus which brings about contraction; division of the motor nerves or interference with their function leads to muscular paralysis, of which the best example in the horse is the left laryngeal paralysis resulting from pressure on the recurrent nerve.

When a muscle contracts it becomes shorter and thicker; the exact microscopical changes which occur are disputed, but no doubt the transverse striæ are brought closer together; after contraction it returns to its original length. Contraction after contraction may be produced, until at last the muscle becomes fatigued; it now contracts more

slowly, and is not capable of performing the same amount of work. If the contractions in a muscle succeed each other with considerable rapidity, there is no period of relaxation, and the part is thrown into a condition of tetanus or cramp. During muscular contraction a sound is produced, which under suitable conditions may be heard.

All these changes can be studied with considerable accuracy by employing muscles isolated from the body, and placed in contact with an apparatus on which they can describe their movements when irritated, and at the same time we can study the electrical phenomena in nerves.

Muscle Currents.—Great controversy has taken place over the question as to whether in muscle, currents of electricity exist independently of those which make their appearance when the muscle is stimulated. It has been found, for instance, that a muscle isolated from the body, and placed under suitable precautions in connection with a galvanometer, demonstrated the presence of electric currents which behaved in a perfectly regular manner, viz., under certain conditions they were always weaker, and under other conditions stronger, in passing from one definite point on the muscle to another. They are spoken of as the natural muscle currents, or the currents of rest, and they always pass in a definite direction, viz., from the surface of the muscle to the cut extremity (Fig. 20). If while the galvanometer is registering the direction of the natural muscle current we stimulate the muscle preparation, a backward swing of the needle of the instrument indicates a current passing in an opposite direction to the natural muscle current: it is termed the negative variation of the muscle current, or the current of action. The existence of currents of rest in living muscle is denied, and it would appear that they are purely post-mortem phenomena, or when obtained in living muscle are the result of injury due to the needful preparation for the experiment.

But there can be no doubt that currents are developed

in muscle during contraction, and these are spoken of as the currents of action.

Currents of action occur during the phase of muscular contraction known as the latent period, a term to be presently described. These currents are not attended by any visible alteration in the state of the muscles, but a contraction follows as the result of their passage; as Foster expresses it: 'they prepare the way for the visible change of form which is to follow.' The current of action travels with

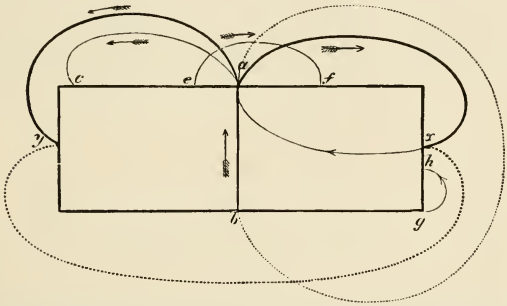


FIG. 20.—DIAGRAM ILLUSTRATING THE ELECTRIC CURRENTS OF REST OF NERVE AND MUSCLE.

Being purely diagrammatic, it may serve for a piece either of nerve or of muscle, except that the currents at the transverse section cannot be shown in a nerve. The arrows show the direction of the current through the galvanometer.

a, *b*, the equator. The strongest currents are those shown by the dark lines, as from *a* at the equator to *x* or to *y* at the cut ends. The current from *a* to *c* is weaker than from *a* to *y*, though both, as shown by the arrows, have the same direction. A current is shown from *e*, which is near the equator, to *f*, which is farther from the equator. The current (in muscle) from a point in the circumference to a point nearer the centre of the transverse section is shown at *g*, *h*. From *a* to *b*, or from *x* to *y*, there is no current, as indicated by the dotted lines (Foster).

great rapidity to the nerve termination in the muscle known as the motor end plate; a contraction now follows, produced by a decomposition of the muscle substance, the contraction being in the form of a visible wave, which leads to swelling and shortening of the muscle fibres.

The electric changes in muscles are practically the same as those occurring in nerves, and as this question has to be dealt with more fully under the nervous system, we shall postpone any further consideration of the subject until then (see p. 255).

A Muscle Curve.—If a muscle preparation be arranged so as to record its movements on a revolving drum, and a single shock from an induced current be passed into it, a single contraction follows which traces an upstroke on the drum, and then the muscle relaxing makes a downstroke; in this way is obtained a muscle-curve. But it is found on examining it that the muscle does not contract immediately the stimulus is applied, but that a perceptible period elapses

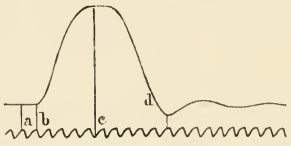


FIG. 21.—A MUSCLE CURVE FROM THE GASTROCNEMIUS OF THE FROG.

a indicates the moment at which the induction shock is sent into the nerve; *b*, the commencement; *c*, the maximum; and *d*, the close of the contraction (Foster).

The curve is read from left to right; below the muscle curve is a curve made by a time recorder, each complete curve representing one-hundredth of a second.

before contraction occurs; this is called the latent period (*a*, *b*, Fig. 21). During this latent period, although the muscle is not moving, yet it is possible to determine that the natural muscle current is diminished and that negative variation occurs—viz., a momentary reversal of the natural current. The latent period differs in various muscles, and depends also on their condition; in the frog it is estimated at $\frac{1}{100}$ of a second. Succeeding the latent period is the stage of contraction, at first slow, then rapid, then again slow till extreme contraction has been produced, followed by the third stage—viz., that of relaxation or elongation of the muscle—which is slow at first and then rapid; while

the fourth stage consists of one or two small curves, due to the elasticity of the muscle, termed the stage of elastic vibration. All these periods are seen in the curve in Fig. 21.

As the muscle becomes fatigued the latent period becomes longer, and the contraction is slower and shorter; fatigue diminishes the elasticity of muscle. If a succession of shocks be passed into the muscle in sufficiently rapid sequence tetanus is produced. On the recording apparatus there is a long sharp upstroke, representing the second stage; the tetanic period is represented by a long irregular line, and when the tetanus passes off there is a sudden relaxation representing the third stage (Fig. 22).

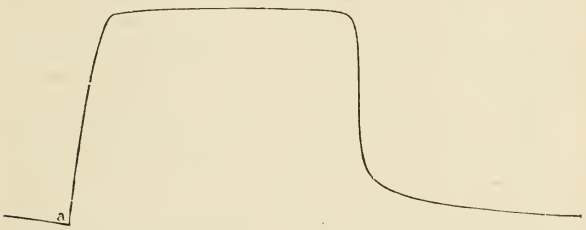


FIG. 22.—TETANUS PRODUCED WITH THE ORDINARY MAGNETIC INTERRUPTER OF AN INDUCTION MACHINE (RECORDING SURFACE TRAVELLING SLOWLY).

The interrupted current is thrown in at *a* (Foster).

The irregular line shows that tetanus consists of a series of short contractions, with an insufficient interval for complete relaxation—in other words, it is not a single long contraction. A muscle cannot continue permanently in a tetanic condition, fatigue occurs followed by relaxation.

Besides electrical stimuli, muscles may be excited by mechanical stimuli—such as a prick or tap—or the application of acids or metals to the muscle, some of which act directly on the muscle substance, others through the medium of the nerve.

Electrical or other stimulation of involuntary muscle behaves much the same as voluntary, excepting that the

contractions are much slower and longer. The intestinal movements seen in a horse recently destroyed exhibit perfectly the latent period, the stage of contraction, and that of relaxation. If the bowels or stomach be very irritable the lightest touch provokes a contraction, and in the case of the stomach particularly, large weals occur on its surface by lightly drawing the finger over it.

The **Elasticity** in muscle depends upon its condition. In a resting muscle the elasticity is small but perfect—that is to say, on being stretched it regains its natural length when released; a working muscle owing to fatigue is less elastic than a resting one. The great advantage to the animal machine of the elasticity of muscles, is the reduction in concussion to the skeleton during progression. The skeletal muscles in the living body are always slightly on the stretch, at any rate they are not slack, as otherwise great loss of time would occur before they could act.

We have certain muscles in the machine where the strain on them is so considerable that tendinous material is intimately mixed up with the muscular tissue; this is well seen in the masseters, the muscles of the back, forearm, and thigh. In the living animal provision is made for the muscles of the limbs being rested without necessitating the horse assuming a recumbent position, viz., by means of the check ligaments in the leg; by this means a horse can sleep standing, and may remain standing for many weeks without suffering.

Muscle Fatigue.—Fatigue in muscle is due to excess of work; the products arising from muscular contraction accumulate faster than they can escape, the irritability of the muscles decreases, and they require a greater stimulus to induce them to respond. The fatigued muscles are also acid from sarcolactic acid, which probably produces the soreness and stiffness resulting from overwork. Hand-rubbing and shampooing the tired body muscles, such as is practised on both man and horse in India, and followed by such good results, is explained by the fact that the lymph vessels are stimulated to further absorption, and the lactic acid and other fatigue products got rid of. This is also

the explanation of the value of hand-rubbing the legs of horses.

Great difference of opinion exists as to whether fatigue begins in the nervous system or in the muscles themselves. I incline to the view that the nervous system fails first.

That remarkable state of the body described as 'condition,' into which horses can be brought by care in feeding and general management, and carefully-regulated work, must be regarded as the highest pitch of perfection into which muscles can be brought; it is not a permanent condition: no horse can remain in it for any length of time, and many can never be got into it at all. It is easy in the training of horses to overstep the mark and produce 'staleness,' a condition due to over-training, but which, unless it be gone too far, is in both men and horses recovered from by a short judicious rest, when the system immediately responds. 'Staleness' must be regarded as having its primary origin in the nervous system.

Laws of Muscular Work.—The material used up in muscle as the result of contraction may be regarded as so much fuel. Looked at from this point of view the muscles are very superior machines, for they obtain from the fuel one-fourth the amount of energy it is capable of producing, whereas the best-made and most carefully-constructed engine, cannot extract from fuel more than one-ninth the energy it is capable of yielding; moreover, the animal machine gets stronger by wear instead of weaker.

The amount of work performed by the body is measured in foot-tons, viz., the number of tons lifted 1 foot high. It is evident that the force which can lift 1 ton 20 feet high would be equivalent to the force which lifts 20 tons 1 foot high (see Locomotion).

The work performed by a muscle is ascertained by multiplying the weight lifted by the height to which it has been lifted.

The following are the laws of muscular work:

1. The larger the transverse section of a muscle, the greater the load it can lift.

2. The longer the muscle, the greater the height to which it can lift a load.

3. A muscle at its first contraction can lift its greatest weight; but as the contraction continues, the weight it can lift becomes less and less.

During progression the entire strain of the body comes on the feet and the muscles of the limbs, and during such paces as galloping the strain is enormous. By galloping a horse over a weigh-bridge, I have observed that a weight equivalent to that of the whole body is imposed on one fore-leg; it is very easy, therefore, to understand why horses break down, for as their muscles become fatigued they lose their elasticity, and the strain is now thrown on the flexor tendons, which possessing but little, if any, elasticity, give way under the weight.

Rigor Mortis.—After death a muscle passes into the condition of rigor or stiffening, by which it changes both in its physical and chemical aspect. The muscle becomes firm and solid, loses its elasticity, and no longer responds to electrical stimuli; further, it loses its alkaline reaction, and in course of time becomes acid, due to the formation of lactic and other acids. Through the death of the muscle the fluid myosin becomes coagulated; it is this coagulation which produces the stiffening. Through rigor mortis heat is developed; some after-death temperatures are remarkably high (see p. 241).

The rapidity with which rigor mortis sets in differs according to the mode of death. If an animal in perfect health be destroyed, the muscle stiffening is slow to set in and very persistent; where death is produced by debilitating disease, or in cases where severe muscular exhaustion has preceded death, the rigor mortis may occur so suddenly and pass off so rapidly as occasionally to escape observation, and decomposition also sets in early. The muscles of the tongue appear to me to be the only ones where rigor mortis does not occur, or only incompletely; the extremity of the tongue in a dead horse is always flaccid, and hanging out of the side of the mouth.

After a certain length of time rigor mortis passes off and decomposition commences.

CHAPTER XV.

THE NERVOUS SYSTEM.

From the fact that the nervous system only occupies a very subordinate position in veterinary medicine and surgery, and also that in the lower animals its functions, so far as the brain is concerned, are so immeasurably inferior to that of man, I do not purpose giving more than an outline of the physiology of the parts concerned so far as it has been ascertained.

The physiology of the nervous system has principally been worked out on frogs, rabbits, dogs, and monkeys. We have no evidence that the various tracks found in the spinal cord of man and dogs exist in the herbivora, though there can be no doubt that some, or perhaps even all, are present; but the inquiry on dogs and rabbits, which have yielded such fruitful results in determining the paths in the spinal cord, have not been experimentally applied to the horse and other large animals, and there are no degenerative diseases of the cord, as in man, pointing to the existence of definite tracks, so that we can only assume the existence of much with which we have to deal. The same may be said of the motor centres in the cerebrum, the knowledge of which is calculated to revolutionize brain surgery in the human subject. Motor areas, no doubt, exist in herbivora, but we have no exact evidence of their position, and even if we possessed this knowledge, could not probably turn it as yet to any useful advantage.

The nervous system is widely distributed throughout the body; there are but few places where no nerves have been

found. It is through the medium of this system that the blood supply to a part is governed, that the tissues are nourished, that the part possesses sensation and power of movement, and that those processes of life are kept up over which we have no control, and of the existence of which, so far as our feelings are concerned, we have but little knowledge; further, it endows the body with sight, touch, smell, and hearing, and furnishes animals with whatever intelligence they are capable of exhibiting. The nervous system of man and the lower animals principally differs on the ground of intelligence; it is this latter which produces in man his great cerebral development, and marks him out as a superior being.

The nervous system is composed of the brain and spinal cord, the nerves with their terminal endings, also a special system of nerves known as the sympathetic. It is necessary to the elucidation of the subject that these should be dealt with in an inverse order, and we have first to inquire into the function and properties of the nerves.

The Nerves.

These form the lines of communication between the tissues and the brain and spinal cord. It is by means of them that sensations arise, that motion is produced, that the calibre of the bloodvessels is regulated, that secretion is brought about, that the contraction of the heart is induced and kept under control, that nutrition is governed, and sight and other special senses produced. Nerves are, therefore, spoken of as sensory, motor, vascular, secretory, inhibitory, trophic, and nerves of special sense. These are further subdivided into those whose duty is to convey impulses from the body to the brain and spinal cord, and hence called centripetal or afferent nerves, whilst those which transmit impulses from the brain and spinal cord to the body are termed centrifugal or efferent nerves.

We have no means of distinguishing these various nerves either by their physical properties or microscopical appearance; and though in the body their activity is exercised

in one direction only, we know that removed from the body, it is just as easy to transmit nervous impulses in one direction as the other; and experimental inquiry has ascertained that it is possible to join a sensory to a motor nerve, and reverse its function,* showing that it is possible in the body to alter the actual current through the nerve.

We have spoken of this as if the exciting influence were due to an electrical current; as a matter of fact, we have no knowledge of the influence which is at work in producing motion as the result of stimulating one nerve, sensation of another, secretion of a third, and so on; but we do know that the irritability of nerves is readily manifested on the application of electrical stimuli, and we may, therefore, at at once consider the changes thus brought about.

Electrical Phenomena of Nerves.—If a nerve be removed from the body and suitably applied to an instrument which is capable of measuring delicate electric currents, the galvanometer, the needle of the instrument will be found to be deflected, showing the passage of a current; it is spoken of as the current of rest, and by many physiologists grave doubts have been expressed as to whether this is a natural current in nerves or not. It is practically identical in direction with the natural muscle current described on p. 246. If while the current of rest is passing a shock be sent into the nerve from an induction coil, the needle of the galvanometer is found to indicate a momentary current in the opposite direction to the current of rest. This momentary opposite current is spoken of as negative variation or the current of action. If now, instead of passing into the nerve a shock from an induction coil, we pass into it a continuous current of voltaic electricity, certain phenomena will occur, to explain which we must suppose the nerve experimented upon to be in connection with a muscle.

The electrical stimulation employed is the make and break of a constant (voltaic) current, such as is produced by connecting two wires with a suitable battery, and an

* This is not generally accepted as correct by physiologists.

induced current (faradic), which is obtained by means of a battery and an induction coil.

If a moderate constant current be passed into the nerve by connecting it with the poles of the battery, at the moment the connection is made the muscle gives a twitch or contraction and then remains perfectly quiet, though the current is still streaming through it; if the connection be broken by removing one pole of the battery, the muscle gives another contraction. This is termed 'a making and breaking contraction,' viz., a contraction produced on closing and opening the electric circuit. If instead of a moderate constant current a weak or strong one be used, the results on making and breaking may not be the same.

During the period of apparent quiescence following the closing of the circuit, though the muscle is giving no indication of the current, yet profound changes are occurring in the nerve; for if it be tested by passing into it an induced current, it is found that the irritability is diminished in the neighbourhood of the positive pole of the continuous current, and increased in the neighbourhood of the negative pole. This is known as **electrotonus**, the diminished irritability being known as **anelectrotonus**, that of increased excitability as **kathelectrotonus.** Between the increased and reduced irritability is a zone of unaffected irritability, known as the **neutral point.**

During the condition of electrotonus there is no interruption to the natural nerve current; provided the constant current takes the same direction as the current of rest through the nerve, the natural current is simply increased; but if the constant current be passing in the opposite direction to the nerve current, the latter is diminished.

To state this matter more clearly, imagine a nerve running to a muscle, Fig. 23; at a certain part of the nerve a continuous current of electricity is passed through it (the application and withdrawal of which gives rise to the making and breaking contraction previously mentioned), but during the passage of the current the muscle is perfectly quiet, in spite of important changes occurring in the

nerve. A shock is now sent into the nerve from an induction coil at a place between the muscle and the continuous current; as the result of the stimulation the muscle either responds more than it should do for the strength of the stimulus employed, viz., there is increased excitability of the nerve (kathelectrotonus), or the muscle does not

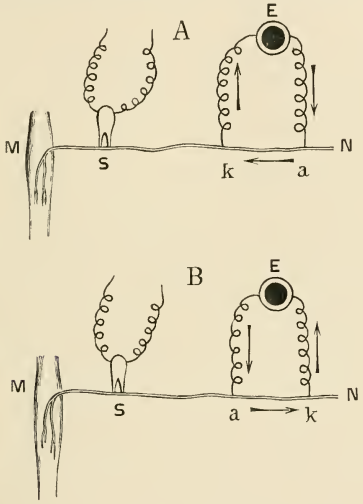


FIG. 23.—DIAGRAM OF ELECTROTONUS.

N, the nerve running to the muscle M; E, an element for the production of a constant current, the positive pole or anode (a) in A being placed furthest from the muscle, the current consequently flowing down the nerve, and in B being placed nearest to the muscle, the current flowing up the nerve; at S the nerve is stimulated by an induced current, and its irritability determined by the contraction of the muscle M; the irritability is increased in A, kathelectrotonus, and decreased in B, anelectrotonus.

respond as strongly as it should, viz., there is decreased excitability of the nerve (anelectrotonus). The increase or decrease of excitability in the nerve depends upon whether the continuous current is passed down it, as in Fig. A, or up it, as in B; with a descending current the excitability is increased, with an ascending one it is decreased.

The explanation of electrotonus in nerves is that it is a vital phenomenon, viz., the irritability of the nerve is increased when its molecules pass from their ordinary condition to one of greater mobility (kathelectrotonus), or it is diminished when its molecules pass from their ordinary condition to one of less mobility (anelectrotonus) (Cyon). Hermann considers that it is a purely physico-chemical phenomenon, due to the electric current generating acids at the positive pole, and alkalis at the negative; the effect of the acid being to lower the excitability of the nerve, and of the alkali to increase it.

The practical application of this law is that the excitability of a part, pain, cramp, etc., may be removed by passing a current up the nerve, viz., by placing the positive pole nearest the muscle, and producing anelectrotonus; or by reversing the process and throwing the current down the nerve, so that the negative pole is nearest the muscle, the irritability of the part is increased.

The **Irritability of Nerves** is increased by electric, thermal, chemical, and other stimuli; it is diminished by cold, compression, or injury; it is exhausted by shock or continual excitement. Nerves are not capable of originating in themselves any impulse; the latter is produced by the impressions made on the nerve terminations. While impulses are being conducted along a nerve, neighbouring nerves, though in contact, are not affected by it. This is probably explained by the fact that each nerve fibre is isolated from its fellow by a sheath, which acts the part of a non-conductor. A nerve cannot be motor one moment and sensory the next. These functions are entirely distinct, and are dependent upon the nerve terminations.

It is necessary for the transmission of an impression that the nerve should be intact from its origin to its destination: division of a sensory nerve means loss of sensation to all parts supplied by it; if the main trunk be divided, entire sensation is lost; if only a branch of the trunk, loss of sensation follows to the part supplied. We see this perfectly demonstrated in the ordinary operation of neurectomy.

If the divided end of the sensory nerve be irritated, that portion still in communication with the spinal cord exhibits signs of pain.

In motor nerves the reverse applies. Division of a motor nerve means loss of power of movement; if that portion in connection with the tissues be irritated, movement results. We shall have to allude to this again in speaking of the spinal cord.

If a sensory nerve be irritated, the pain is felt in the whole part supplied by that nerve and its branches; and if the motor nerve be irritated, the whole of the parts supplied by this nerve and its branches exhibit movement. In the same way division of a secretory nerve means loss of secretion; irritation of the extremity still in contact with the gland means increased secretion. Division of a trophic nerve may or may not be followed by loss of nutrition, as witnessed in the comparative rarity of sloughing of the foot after neurectomy.

The effect of dividing nerves is degeneration of that portion either above or below the injury. Thus division of a sensory nerve above the spinal ganglion causes degeneration of that portion still in connection with the spinal cord; whilst division of a motor nerve means degeneration of that still in connection with the tissues. In this way it has been determined that the nutrition of sensory nerves comes from above, whilst the nutrition of motor nerves comes from below the cut extremity.

Nerves are probably nourished by the plasma which reaches the axis cylinder at Ranvier's nodes (M'Kendrick).

The rate of transmission of impulses through human motor and sensory nerves has been placed at 111 to 140 feet per second.

In visceral nerves the velocity is less. Chauveau ascertained that in the pharyngeal branches of the vagus the velocity was 26 feet per second.

Ganglia.—On certain nerves are to be found nodules termed ganglia; they are abundant in the nerves of a system which we have yet to consider, viz., the sympathetic;

on the cerebro-spinal nerves they are to be found, though in all cases limited to the sensory branch only. The structure of the ganglia of a sympathetic and cerebro-spinal nerve is not identical: in the former the nerves composing it are both medullated and non-medullated, and the nerve cells of the ganglia are multipolar; in the cerebro-spinal ganglia the nerve cells are only unipolar, and the nerve fibres medullated on entering, but non-medullated on leaving it. The one pole or process issuing from the nerve cell after a time divides forming a T-piece, one end of the T probably running to the nerve centre, and one to the periphery. The cells are really lateral appendages to the fibres, and we again repeat they are found on sensory and not on motor nerves. The only known function of ganglia, whether cerebro-spinal or sympathetic, is for the purpose of nerve nutrition; no impulses originate in ganglia, nor can they serve as centres for reflex action; in other words they are not nerve centres.

Nerve Terminations.—We have alluded to the terminal end organs of nerves, and attributed to these the special function of the nerve; we must therefore briefly refer to them. A well-known form of nerve termination is the Pacinian corpuscle; it is found both in connection with cerebro-spinal and sympathetic nerves. Touch corpuscles are found in the muzzle of the horse and other animals, and probably also in the sensitive structures of the foot; end bulbs are found in the generative organs; bodies like Pacinian exist in tendons; besides these, there are motor terminations, such as the motorial end plates in muscle, and secretory fibre terminations in the various glands; lastly, there are endings in the nerves of special sense, such as the rods and cones of the retina, etc.

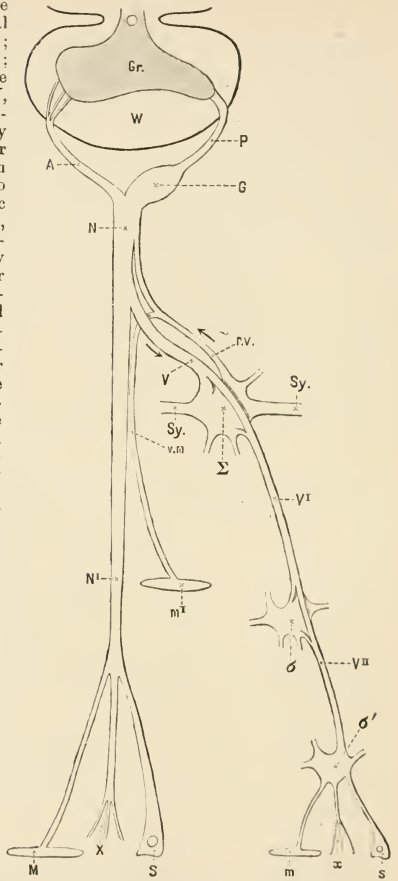
Spinal Cord.

The spinal cord extends from the atlas to about the second or third sacral vertebra. It is completely enclosed by a dense membrane, the dura mater. The canal in which it is lodged is very much larger than the cord, especially at

those parts where the greatest amount of movement occurs, as in the neck. The cord is not the same shape nor the same size throughout; oval in the cervical region, it becomes circular in the dorsal, and again oval in the lumbar portion. It is largest where any considerable bulk of nerves is being given off, and thus there is an enlargement corresponding to the fore, and another to the hind limbs. We speak of the superior and inferior face of the cord, or perhaps it would be more in accordance with comparative anatomy to describe it as the dorsal and ventral face or surface. On exposing the spinal canal, a large number of nerves are found to be passing through the dura mater, either outwards or inwards, and these gain an exit from or entrance to the spinal canal by means of the foramen formed at the juncture of the vertebræ.

On opening the dura mater, it is easy to determine that the nerves divide in such a way that part of them run to the upper or superior surface of the cord, and part to the inferior. These are spoken of as the superior and inferior spinal nerves. In the horse the number of branches of nerve thus formed is considerable, for both the superior and inferior enter the cord not by a single root, but by several. On the superior roots, but outside the dura mater, is found a nervous body termed a ganglion; each of the branches of the several roots of a superior spinal nerve has a ganglion on it. No such ganglion exists on the inferior root, but inferior and superior roots unite after passing the ganglion to form a mixed spinal nerve (see Fig. 24). The function of these two sets of nerve roots is entirely different. The superior root, containing the ganglion, conveys sensation and sensation only; the inferior roots convey motion, in addition to certain other functions to be shortly alluded to; the superior roots are passing into the cord, the inferior roots are passing out of it. Passing out with the inferior root of the spinal nerve, but indistinguishable from it, is a branch of nerve known as the white ramus communicans, which leaves the main trunk after the mixed nerves have formed, and runs to a distinct system known

FIG. 24.—SCHEME OF THE NERVES OF A SEGMENT OF THE SPINAL CORD (FOSTER).



Gr., grey; W, white matter of spinal cord; A, inferior; P, superior root; G, ganglion on the superior root; N, mixed nerve, consisting of sensory and motor branches with fibres passing into the sympathetic system at V; N^1, spinal nerve, consisting of sensory and motor branches, terminating in M, skeletal muscles. S, sensory cell or surface, X, in other ways; V, white ramus communicans uniting the cerebro-spinal with the sympathetic system, running out from the cord with the inferior spinal nerve, and given off from the mixed nerve at V, from whence it passes to Σ, a ganglion on the sympathetic chain, and passing on at V^I to supply the more distant ganglion σ, then at V^{II} to the peripheral ganglion σ, and ending in *m*, a visceral muscle, *s*, a visceral sensory cell or surface, *x*, other possible visceral endings.

From Σ is given off a branch, r.v., known as the grey ramus communicans, which partly passes backwards towards the spinal cord, and partly runs, as v.m., in connection with the spinal nerve to supply vaso-constrictor fibres to the muscles, m^1, of bloodvessels in certain parts, for example, in the limbs.

Sy, the sympathetic chain (gangliated cord of the sympathetic) uniting the ganglia of the series Σ. The terminations of the other nerves arising from Σ, σ, σ', are not shown.

as the sympathetic; one part of the latter, the gangliated cord, runs under the arch of the ribs and back as far as the loins; to this cord the white ramus runs, and establishes a communication between the cerebro-spinal and sympathetic system; moreover, in this branch are the nerves which constrict all the bloodvessels in the body. A careful study of Fig. 24 is necessary for clear elucidation of the arrangement of the spinal nerves.

Arrangement of the Cord.—If a cord be suitably prepared, it is found to consist of a superior, lateral, and inferior column, each divided by a longitudinal groove. On the superior and inferior surface is a fissure: the inferior fissure is wide, and does not reach down to the centre of the cord; the superior fissure is very narrow, and so deep that it runs down into the central portion of the cord.

On making a section of the cord, it is found to be made up of both white and grey matter, the latter internally placed, forming the medulla, is arranged something like two commas placed back to back, the tail of the comma being uppermost; the tail of the comma corresponds to the incoming sensory fibres, the head of the comma to the outgoing motor ones. The two commas are connected by a band of grey matter, known as the commissure, in the centre of which is a canal.

Speaking roughly, we may say that the white substance of the cord is made up of fibres, the grey substance of nerve cells. The white substance is not the same thickness throughout, the upper portion of the cord containing more white matter than the lower portion. In the same way, the grey substance is not the same thickness nor the same shape throughout the length of the cord. This grey substance is very important. We shall have to show that directly or indirectly both the superior and inferior nerve roots communicate with it. The nerve cells composing it are multipolar and of considerable size, each containing nuclei with nucleoli. It has been ascertained that the nerve cells of the grey matter are unequally distributed, and can be grouped according to their position; thus, in

the inferior portion of the inverted comma, or, as we shall speak of it, the inferior cornu, they are exceedingly numerous, there being five groups of nerve cells each known by a separate name; whilst the cells of the superior cornu are not only fewer in number, but the number of groups is only three or four.

Tracts in the Cord.—The white matter of the cord can be mapped out into columns or tracts, which are quite distinct from the columns into which the cord is originally

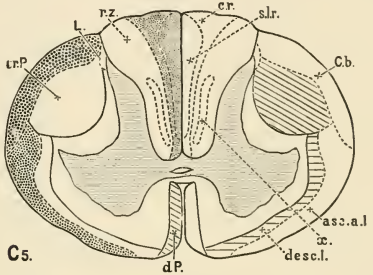


FIG. 25.—DIAGRAM TO ILLUSTRATE THE GENERAL ARRANGEMENT OF THE SEVERAL TRACTS OF WHITE MATTER IN THE SPINAL CORD.

The ascending tracts are shaded with dots; the descending tracts are shaded with lines. The shading is in each case put on one side of the cord only, the reference letters being placed on the other side. cr.P, pyramidal tract; dP., direct pyramidal tract; C.b., cerebellar tract; s.l.r. and c.r. together indicate the median posterior tract (tract of the fibres of the superior or sensory roots of the spinal nerves); asc.a.l., the antero-lateral ascending tract; desc.l., the antero-lateral descending tract. (Foster, after Sherrington.)

divided. Some of these tracts are supposed to be conveying impulses from the cord to the brain, and are known as ascending tracts; others are conveying impulses from the brain to the cord, and are known as descending tracts. These descending and ascending tracts have not been made out by ordinary observation, but by experimental inquiry. It was found that after division of certain nerves or injuries to certain parts of the brain, particular tracts became de-

generated either in an upward or downward direction. By this and other means, it was ascertained that certain paths or tracts exist in the white matter of the cord, connecting the brain with the cord and *vice versâ*. It must not be supposed that the function of a downward or upward tract is entirely exerted in the direction given to it by its name; they are called upward or downward depending upon the direction of the degeneration resulting from experimental injury.

The following are the tracts in man according to Foster:

Descending Tracts.	*Ascending Tracts.*
Pyramidal tract.	Cerebellar tract.
Direct pyramidal tract (not found in animals).	Median posterior tract.
Antero-lateral descending tract.	Antero-lateral ascending tract.
Comma tract (limited to cervical and upper thoracic regions).	

These paths, known to various observers by somewhat different names, are distributed between the anterior, lateral, and posterior columns; an examination of the diagram (Fig. 25) will render their position in the cord more clearly understood. These tracts are not found throughout the entire length of the cord, and in all cases they diminish in size from the head to the tail.

The pyramidal tract is large in man but small in the monkey and dog; it is in connection with the motor region of the brain, and its great size in man appears to bear a distinct relation to the complexity of the motor region: the more intricate the changes in the central nervous system the larger the pyramidal tract. (Foster.)

Some of the tracts run from the white and terminate in the grey matter. The tracts differ microscopically, some being composed of coarse fibres, others of fine, some of mixed fibres.

It has not been found possible to divide the whole of the white matter into tracts; even after all the above have been defined, there is still much left unaccounted for.

When the various tracts in the spinal cord reach the medulla they undergo change in form, position, and distribution, in order that they may arrive at the various parts of the brain to which they are proceeding. This will be alluded to again when speaking of the medulla; but we may here mention that only two unbroken spinal tracts pass through the medulla to the higher centres, all the others being broken up.

The conducting paths in the cord will be studied presently, when we have learned the functions of the spinal nerves and of the nerve centres.

Spinal Nerves.—We must now describe very briefly how the nerves entering and leaving the spinal cord are disposed with reference to the cord itself.

The superior or sensory roots enter the cord just by the upper cornu; some of the fibres run up, and some down the cord for a short distance, and then pass horizontally across it. Other fibres enter the white instead of the grey substance, and after passing some distance up the superior columns of the cord enter the grey matter. The connection between the sensory nerves and the cells of the grey matter of the superior cornu, is by no means so definite as the connection of the motor nerves with the grey matter of the inferior cornu. The motor nerve, or inferior root, is continuous with the axis cylinders of the cells of the inferior horn, though some fibres may be found to be in connection with the white matter of the lateral columns; these later on cross over the cord and enter the grey matter of the inferior cornu of the opposite side.

The chief difference in the behaviour of the two roots is that the inferior is in direct connection by means of their axis cylinders with the nerve cells of the inferior cornu, whilst the superior root is only in connection with the nerve cells of the superior cornu, by means of a network of nerve tissue known as Gerlach's.

If the sensory root before entering the cord be divided above the ganglion, its division causes pain; irritation of the distal extremity causes no sensation, whilst irritation

of that part still in connection with the cord, the proximal end, produces pain. In course of time degeneration of the nerve and the tracts in the cord supplied by it occurs; but the proximal, and not the distal, end is the part which undergoes degeneration. If the nerve be divided below its ganglion, then degeneration of the nerve below the ganglion occurs. This is explained by saying that the ganglion is the seat of nutrition of the sensory root. Another result of the division of this root is loss of all feeling in the parts supplied by it. When the inferior or motor roots are cut, movement of the parts with which it is in connection occurs; stimulation of the proximal end produces no movement, whilst stimulation of the distal extremity provokes muscular contraction; as the result of the section degeneration occurs, not, however, on the spinal cord side of the nerve, but in the distal extremity. On irritating the proximal extremity of the divided motor roots, it has been found in some cases that pain results. This is due to the fact that some sensory fibres are also present in the inferior root, being derived from the superior one after the nerves have joined. The phenomenon is termed recurrent sensibility.

The function of the inferior or motor roots is to supply all the voluntary muscles with the power of movement, the bladder and uterus with contractile power, dilator and constrictor fibres to the bloodvessels, secretory fibres to the sweat-glands of the skin, and nutritive nerves to the tissues. The spinal sensory fibres supply sensation and touch to the whole of the body, with the exception of certain parts of the face.

The vaso-motor fibres run in the lateral columns, passing into the ganglia of the grey matter; they leave the spinal cord by the inferior root, and reach the muscular coat of the bloodvessels either by the spinal nerves or the sympathetic. Respiratory nerves run down the lateral columns on the same side as the centre from which they originated, and pass through the inferior roots to the motor nerves of the respiratory muscles.

Between the spinal cord and the sympathetic system are chains of fibres connecting the two; these fibres originate in certain columns of the cord, pass out through the intervertebral foramen, and so establish a communication between these two important nervous systems (see p. 261).

In order that we may understand the functions of the nerves and spinal cord, it is necessary that the complex acts which they are capable of producing should now be dealt with.

Nerves by themselves are not capable of generating any impulses; they must be in connection with a nerve centre. We have seen that the spinal nerves are in connection with nerve centres in the spinal cord and brain, and we have now to learn the nature of the various impulses these are capable of causing.

Reflex Action.—When a horse endeavours to save himself from falling the act is a purely reflex one—that is to say, whether he voluntarily tries to save himself or no the result is the same, viz., the effort is made; he becomes conscious of the effort, but only after it is completed. When the eyeball is touched with the finger it is withdrawn into its socket, the membrana protruded, and the eyelids closed; this is a purely reflex act, and may be found to occur immediately after death produced by section of the medulla; with the exception that the eyelids are not closed, the act in all other respects is as perfectly performed as during life. If the hand be suddenly raised as if to strike a blow in the face, the eyelids blink, and by no effort of the will can this under ordinary circumstances be prevented, though the horse may know through repeated attempts that no blow will be inflicted; the rapid closing of the lids is a reflex act.

The main feature of a reflex act is its apparently intentional character. By means of the sensory nerves the impression is conveyed to a nerve centre, and in this place certain changes rapidly occur which lead to impulses passing out along the motor nerves. The changes in the nerve centre are probably of a highly complex kind. The

impulse along the sensory nerve is not simply reflected into a motor channel, as the name would imply, and therefore the term 'reflex,' though retained by custom, is not a correct explanation of what really occurs.

Other reflex acts are still more complicated, as in walking, trotting, etc. Here the animal is completely unconscious of the various groups of muscles to be brought into play; the whole process is carried out independently of consciousness—in fact, if the horse had to think of each step to be taken, it would soon be worn out and certainly blunder.

So far the illustrations we have given of reflex action are those resulting in movement; but a reflex act is not essential a motor act, it may be a secretory or a nutritive one, depending on the character of nerve sending out the efferent impulse. In order, therefore, that a reflex act may be accomplished certain conditions must be present: (1) an afferent nerve, to convey the impression to the nerve centre; (2) a nerve centre, in which the outgoing impulses are generated; (3) an efferent nerve, to convey these impulses outwards.

It must not be considered that reflex actions can only take place along nerves belonging to the same system; the afferent or efferent nerves may be both cerebro-spinal, or one or the other may belong to the sympathetic system, or both may belong to the sympathetic system.

It is by the regular and apparently intelligent carrying out of reflex actions that the normal condition of the body is maintained. Swallowing, secretion of saliva, gastric juice and other fluids, respiration, intestinal movements, etc., are all examples of this condition.

There are certain reflex acts of which the animal can take cognizance, though it can take no part in them. These are termed 'sensori-motor'; those which it is unable to perceive are spoken of as 'excito-motor.'

There are certain reflex movements in man which are acquired only as the result of education—for example, walking. In animals these so-called co-ordinated reflex

actions are rapidly acquired—in fact, would appear to be more highly developed, in the same way that the limbs are more developed in the foal than in the child. In the former, for instance, the limbs from the elbow and stifle to the foot are nearly their full length very shortly after birth, and such joints as the hock are almost the same size as at maturity.

There are other functions of nerve centres which possess perhaps a greater pathological than physiological interest, viz., the **transference** and **radiation of impressions.** An impression is transferred, when the animal instead of perceiving it as arising from its proper place, believes it to exist in another position. Here the efferent impression, instead of being conducted back from the nerve centre to where the afferent impulse arose, is perceived in another position; thus thirst is referred to the fauces, colic is referred to the abdominal walls, etc. Some forms of liver disease in the horse have been known to cause lameness in the off fore-leg, evidently referred to the shoulder as in the human subject, in whom also stone in the bladder causes pain in the end of the penis.

By the radiation of impressions is understood the feeling which refers the impression from a part to exist over a much larger area than that from which it is derived—a familiar example in ourselves is the diffused pain of toothache. In the horse a not uncommon example is the pain found in the leg, generally over the flexor tendons, when pus exists in the foot; also the diffused pain of colic, though probably the irritating area may be only a few inches in length.

The majority of physiologists have ceased to describe the radiation and transference of impressions; I have introduced them here owing to their clinical interest.

Other functions of nerve centres are **Automatism, Augmentation, Inhibition,** and **Co-ordination.** By automatism we understand the power possessed by a nerve centre of originating impulses on its own account without any previous stimulation. The nerve changes resulting in the

respiratory movements and the contraction of the heart are automatic impulses.

Augmentation and inhibition in a nerve centre is the power it possesses of increasing or decreasing a reflex or automatic movement.

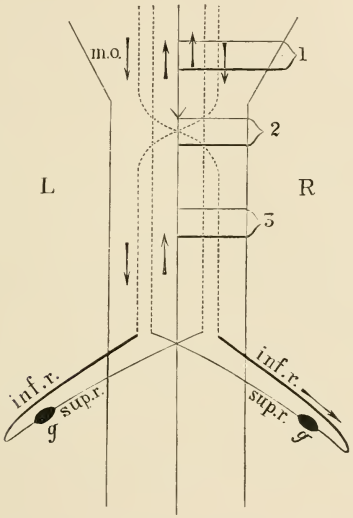


FIG. 26.—DIAGRAM OF THE DECUSSATION OF THE CONDUCTING PATHS IN THE CORD FOR SENSATION AND VOLUNTARY MOVEMENT.

R, right side; L, left side of cord. *Sup. r*, superior root with its ganlion *g*, the fibres crossing over to the opposite side of the cord and so reaching the medulla *mo*. *Inf. r*, inferior root, the path for which decussates in the medulla and runs down the same side of the cord. The arrows indicate the direction of the nervous impulses. The places, 1, 2, 3, indicate the effect on motion and sensation of sections made in one-half of the spinal cord at different levels. (After Brown Séquard, and Kirke.)

By **Co-ordination** is understood the impulses proceeding from nerve centres which regulate the action of a part, and assist in producing a proper sequence of events: for example, in walking the contraction of groups of muscles

in an exact and regular order is essential, and the same remark applies to swallowing, and the muscles used in respiration and other similar acts.

Conducting Paths in the Cord.—We must now examine the paths by which impressions are conveyed between the body and the brain, and *vice versâ*.

Sensory impressions enter the cord at the superior roots, and pass for a short distance along the superior columns; they then enter the grey matter, passing through the ganglion cells, and cross to the opposite side of the cord (Fig. 26); from here they pass once more into the white substance. It is supposed that, depending on the nature of the impression, the path by which it enters the brain varies, pain being conveyed by one of the white lateral tracts of the cord; touch, temperature, pressure, and muscular sensibility by one of the superior tracts. In this way the impression passes along the cord on the opposite side (excepting muscular sensibility, which is on the same side) to that on which it entered, and so enters the brain. Here the impression is made and a motor impulse is generated, which, passing out of the brain into the medulla, crosses over either in this or the pons, and passing down the pyramidal tracts joins the motor or inferior spinal root (Fig. 26); some sensory impressions instead of crossing in the medulla cross in the cord. The conductors of muscular sense, besides travelling up the same side of the cord on which they entered, do not decussate in the cord but in the medulla. Complex co-ordinated movements are supposed to be capable of being set up in the grey matter of the inferior cornu, either in response to an impression from the brain, or as a reflex act brought about by the sensory nerves passing to the cord.

Having learned the arrangement of the nerves and spinal cord and the functions of nerve centres, we have next to consider the functions of the spinal cord itself.

The Functions of the Spinal Cord are to transmit motor and sensory impulses between the body and the brain, not only up and down the cord, but from side to side. It is the chief centre of reflex actions, both with and without

the assistance of the brain; and it preserves by its automatic action both muscular and arterial tone. In speaking of the automatic action of the spinal cord, it is necessary to remember that it can originate no impulses in the same way that the brain does, and that automatic action in the cord is due to afferent impulses.

The cord is not one large centre, but a series of centres lying end to end, each capable to a greater or less extent of acting independently of its neighbour, and each centre possessing its afferent and efferent roots. The white substance may be regarded as the communicating paths between the cord and the brain; the grey matter as essentially the seat of reflex actions. Experiment has shown that both the grey and white matter is devoid of sensibility. The ganglion on the superior root of the spinal nerve is not a centre for automatic or reflex action, and the same may be said of all other ganglia, cerebro-spinal or sympathetic.

So long as the pathways to the brain are open to sensory and motor impression, so long is the animal capable of performing movements and recognising sensation; but if by operation or accident a part or the whole of the cord be severed, certain symptoms of what we speak of as paralysis appear; whether this occurs to the right or left of the body depends upon the part injured. If the injury be inflicted above the decussation, at the extreme superior part of the cord, a right cord lesion leads to paralysis on the left side, both sensory and motor; if below the decussation, the motor paralysis corresponds to that side of the cord injured, and loss of sensation occurs on the opposite side (see Fig. 26). Loss of motion may not occur immediately after an accident or injury to the spinal cord; but this is accounted for by the fact that the movements observed are not those performed through any intelligent action on the part of the animal, but by reflex action through the spinal centres below the injury. These reflex actions are seen very perfectly in the frog, where after destruction of the brain, some of the actions appear to be produced as if by reason or consciousness. The most remarkable of these experiments is that per-

formed by touching the skin of the body with an acid. The animal endeavours to wipe the acid away with the leg nearest to the injury; and if this leg be secured the opposite one is used for the same purpose. We see nothing so marked as this in the higher animals, though very characteristic reflex actions occur in the dog after division of the cord. It is certain that in the horse, for example, severe injury to the cord may not immediately cause entire loss of motion, though sensation be lost. I have known a horse walk some distance after a comminuted fracture of the dentata, and another to walk a short distance and stand a considerable time, and even to kick, after a fracture of the sixth dorsal vertebra. There can be no doubt, I think, that the spinal reflexes in the larger animals are by no means so well marked as in the dog or in the frog.

The muscle and tendon reflexes, so well known in the human subject, have not, so far as I am aware, been studied in the herbivora; nor do I know whether their existence has been demonstrated, if, perhaps, I except the immediate lifting up of the foot, which generally follows pressure on the so-called 'chestnut' found on the inside of the fore-arm of the horse.

A controlling influence may be exercised over certain reflex acts in the human subject, which are the outcome of moral control, and so have no counterpart in veterinary physiology.

Under the influence of tetanus and the action of strychnia, the reflex centres in the cord are so easily excited that even a slight noise is sufficient to produce those purposeless muscular movements termed convulsions.

Centres in the Cord.—Certain centres exist in the spinal cord for the performance of functions, some of which are partly under the control of the will, whilst the majority are not. It is quite possible for the centres to act by themselves, but under ordinary circumstances they are controlled by higher centres in the medulla.

The **cilio-spinal** centre has for its function the dilatation

of the pupil; it is found low down in the cord, between the cervical and dorsal portion.

The **ano-spinal** centre, found in the lumbar portion of the cord, controls the act of defæcation; it would appear to be highly developed in herbivora, which possess the power of bringing it into play not only when the body is at rest, but during movement. The functions of the ano-spinal centre are rather complex, inasmuch as it has to maintain the tone of the sphincter, and also, on receiving the needful sensory impressions from the bowel, to relax the sphincter, contract the wall of the intestine, and cause a contraction likewise of the abdominal muscles.

The **vesico-spinal** centre, which also exists in the lumbar portion of the cord, governs micturition; its action is like that of the ano-spinal centre.

The **erection centre** lies in the lumbar cord; the **genito-spinal centre** contains the nervous apparatus employed in the emission of semen; the **parturition centre** is situated in the lumbar part of the cord.

Vaso-motor centres, both constrictor and dilator, are found throughout the cord; they are principally under the control of similar centres in the medulla, but may act independently. Sweat centres are probably closely connected with the vaso-motor centres. Trophic centres for the nutrition of the tissues also exist in the cord; destruction of parts by ulceration follows injury of the trophic nerves.

Centres for the maintenance of muscular tone exist in the cord; by means of them the muscles are kept taut and ready for immediate action.

Medulla Oblongata.

Situated at the top of the spinal cord, and forming the connection between it and the brain, is the medulla oblongata. It is composed of white and grey matter, but not arranged with the regularity found in the cord. The columns of the latter are continued into it, and give rise to certain columns in the medulla larger and more prominent

than those of the cord. The inferior spinal columns form the inferior pyramids of the medulla, the superior form the superior pyramids, and the lateral columns dividing into three parts help to form the restiform bodies.

As each of the main paths or highways in the cord are either going to or coming from the brain, it is interesting to briefly understand their distribution.

The pyramidal tract of the cord divides in the medulla into three paths; one proceeding to the motor areas in the cerebrum, one to the cerebrum itself, and one to the corpora quadrigemina. The cerebellar tract of the cord passes through the medulla, and so reaches the cerebellum. The antero-lateral columns run also to the cerebellum, whilst the superior column of the spinal cord divides in the medulla into three paths, two to the cerebellum, and one to the cerebrum; in this way each pathway in the spinal cord finds either an origin or termination in the brain.

The grey matter of the cord does not maintain its characteristic appearance in the medulla; owing to the decussation of fibres in the inferior pyramid the grey and white matter get mingled up, and nuclei and masses of nerve cells are formed as the result. From these nuclei nearly all the cranial nerves arise.

The various tracts passing through the medulla are composed of motor and sensory nerves, or, more correctly, afferent and efferent nerves; both of these decussate in the medulla. But, in addition to these, we have reflex and other centres so numerous and widespread, that it is remarkable how the varied functions carried out by them can be performed within such a limited area.

The decussation of the motor tracts, as previously mentioned, causes a right brain lesion to produce a left body paralysis; and as the sensory fibres decussate in the cord, as described when speaking of the spinal cord, insensibility of the left limbs would result from injury or disease of the right brain (see Fig. 26).

Centres in the Medulla.—The various centres found in the medulla are of such importance to life that an injury to

this part generally means instantaneous death. The whole of the brain may gradually be removed without destroying life, but the medulla will not tolerate such interference. The centres found in the medulla are those for mastication, swallowing, vomiting, respiration, coughing, movements of the heart, bloodvessels, and iris, secretion of saliva, the diabetic centre, and a centre for the sweat glands of the head.

The **mastication** and **swallowing centre** has for its afferent nerves the inferior division of the fifth, glossopharyngeal, and the superior laryngeal of the pneumogastric; whilst its motor branches are in the motor parts of the fifth for swallowing, and in the facial for mastication. It would appear that the reflex act of swallowing may be excited not only by the presence of food in the pharynx, but even by irritating portions of the respiratory apparatus; touching the rima of the glottis excites the act, and so does touching the interior of the trachea, even as low down as the bronchi. A **vomiting centre** exists in the medulla, which in the horse and ruminants is certainly most imperfectly developed. We have previously, p. 137, drawn attention to the fact that there is no drug which has the power of exciting vomiting in the horse; tartar emetic has not the slightest action, and the effect of apomorphia is only to produce the most alarming symptoms of cerebral excitement, but no attempt at vomiting. **Secretion of saliva** is influenced by the chorda tympani, which has its origin in the medulla (see p. 105). A **centre for dilating the pupil** also exists, the fibres for which are contained in the third nerve, and through the sympathetic with the cilio-spinal centre in the cervical cord.

Other centres in the medulla depend upon automatic action, for example, the respiratory and cardiac centres.

The **respiratory centre** is situated close to the origin of the pneumogastric nerves, and is divided into an expiratory and inspiratory portion. The afferent nerve is chiefly the pneumogastric; but no doubt a large number of other nerves may indirectly take part in the action, as is witnessed in

the inspiratory efforts of the nostril and mouth when the medulla is divided, or in the sudden gasping produced by throwing cold water on the body. The chief efferent nerve is the phrenic, the diaphragm being the principal muscle of inspiration. The vagus has a twofold action on respiration, being capable through certain fibres of increasing and through others of decreasing respiration. It is believed that impulses conveyed through the vagus to the medulla excite the inspiratory portion of the centre, whilst others passing into it through the superior laryngeal excite the expiratory portion. This view of the matter must not be too rigidly adopted. Another view is that during inspiration dilatation of the lungs mechanically stimulates certain nerves, which convey to the medulla through the vagus expiratory stimulation, and conversely during expiration mechanical stimulation of the inspiratory centre occurs. This is termed the self-adjusting mechanism.

An inhibitory influence is exercised over the respiratory centre, through influences conveyed to it by either the superior or inferior laryngeal or both, for stimulation of these divided nerves, from that end still in contact with the brain, produces a considerable fall in the number of respirations, and even arrest of them during expiration; on the other hand, stimulation of the cut end of the vagus (from that end still in contact with the brain) produces rapid inspiratory efforts, and therefore may possibly inhibit the expiratory centre. The respiratory centre is stimulated by blood containing a reduced proportion of oxygen, and it is this which largely influences the automatic action of the medulla (see p. 91).

Division of the cord above the origin of the phrenic, it is said, produces death by suffocation, though judging from experiments on the division of the phrenic in the horse, the suffocation is not produced by paralysis of the diaphragm alone, but by paralysis of diaphragm and chest walls (see p. 92); fracture of any vertebra above the phrenic does not necessarily mean immediate death, unless the cord be extensively damaged.

Above the respiratory centre is the **coughing centre.**

In the medulla is situated a **cardio-accelerator** and **cardio-inhibitory** centre. The contraction of the heart is regulated by nerves passing from a centre in the medulla; one nerve, the vagus, passes down the neck, the function of which is to inhibit or restrain the action of the heart; it is brought into action either by automatic impulses originating in the medulla through the blood circulating in it, or reflexly by impressions from without, and it is always in operation. Accelerating influences, from a centre in the medulla, pass to the heart through the sympathetic, the fibres for which issue from the spinal cord in the lower cervical or anterior dorsal region, and pass to the inferior cervical ganglion and then to the heart; the impulses which accelerate the heart are not in constant action (see p. 59).

A **vaso-motor** or **vessel-moving centre** is situated in the floor of the fourth ventricle; by some it is considered to consist of two parts, a vaso-dilator and a vaso-constrictor centre. The vaso-constrictor centre is constantly keeping the vessels in the condition known as 'tone'; if the centre be irritated, the vessels contract and the blood pressure rises. Under the influence of the vaso-dilator nerves, the vessels dilate and the blood pressure falls (see p. 72).

The vaso-motor centre is influenced not only through the cord from below, but directly by the brain from above; it is also stimulated by the character of the blood circulating in the medulla, and under all circumstances it exercises a control over the vaso-motor centres in the cord.

Diabetes, after puncturing the floor of the fourth ventricle, is said to be explained by injury to the so-called dilator centre, allowing the vessels of the liver to dilate (see p. 167). The cause has, however, not as yet been clearly made out.

The **sweat centre** is stated to govern the sweat centres in the spinal cord, and to produce sweating of the head; it can be excited reflexly or automatically.

The **medulla** has no sensation; it can originate no voluntary impulse; it forms a pathway to the brain for the

columns in the spinal cord; gives origin to all the cranial nerves but those of smell, sight, and the motor nerves of the eyeball; it is the head centre for the nerves governing respiration, circulation, the action of the heart, and the digestive apparatus from the mouth to the stomach.

The **Pons Varolii** has no definite claim to be considered as a nerve centre; its use is to conduct sensory and motor impressions to and fro and up and down; it connects the brain with the medulla and cerebellum; when stimulated, pain and muscular spasms are produced. Several of the cranial nerves obtain connection with the grey matter of the various nuclei found in it.

The **Crura Cerebri** connect the cerebellum with the cerebrum, and the basal ganglia with the pons and medulla. They conduct both sensory and motor impulses, and are connected with the complex movements of the eyeball. Division of one peduncle leads to what is known as circus movements, the animal travelling round and round in a circle towards the opposite side to that on which the injury was inflicted.

The basal ganglia have next to be considered; they are composed of the **Corpora Quadrigemina, thalami optici,** and **corpora striata.** The corpora quadrigemina are composed of two parts; an anterior and posterior pair, termed the 'nates and testes.' Destruction of the corpora causes blindness; removal of one part causes circus movements or rolling, or, at any rate, destruction of equilibrium and want of muscular co-ordination; not that these results are confined to the corpora quadrigemina alone, for the same inco-ordinate movements will occur on injury to the crura cerebri, optic thalami, corpora striata, etc. Irritation of the corpora quadrigemina causes contraction of the pupil, whilst removal of these bodies produces dilatation.

The **Thalami Optici** are connected with vision; but are mainly supposed to be the centres for tactile impressions which they transmit onwards to the cerebrum.

The **Corpora Striata** are interesting clinically on account of the comparative frequency with which they are diseased

in the horse. They are considered to be the centres for co-ordination of motor impulses; when they are destroyed the animal has an irresistible tendency to move forwards.

I have certainly seen this latter symptom shown in the horse in disease of the corpora striata, but it is far from invariable. It is remarkable how extensively the parts may be affected and pressed upon by tumours without symptoms being exhibited; the gradual pressure or destruction may account for this.

Cerebellum.

In the cerebellum is found a collection of fibres and ganglion cells, in direct communication with the medulla and cerebrum. It is the first piece of nervous tissue we have studied where the surface has been folded and doubled in on itself to a considerable extent, forming the so-called convolutions; it is composed of grey and white matter, the grey being externally placed and not internally as in the cord.

The functions of the cerebellum are principally concerned in the co-ordination of movement, viz., harmony and rhythm in muscular actions. It is enabled to carry out this function through its connection with the superior columns of the cord, which keep the cerebellum informed of the position of the limbs. There can be no doubt that in co-ordinating muscular movement, the cerebellum is assisted both by the sense of sight, and by the lymph in the semicircular canals of the ear. An animal walks with uncertainty when the eyes are covered up, and disease of the internal ear is a well-known cause of vertigo in the human subject.

The cerebellum possesses no sensation; it is essentially a motor apparatus. When sliced away in birds they lose the power of flying, walking, or preserving their equilibrium; there is no loss of consciousness or intelligence, but an inability to co-ordinate the skeletal muscles. Injury to one of the crura of the cerebellum produces what is termed 'forced movements'; the animal rolls over and over around the long axis of the body, and always from that side on

which the injury has been inflicted, or else circus movements or somersaults are performed.

Cerebrum.

It has been considered that the larger the proportion between the weight of the body and that of the brain, the less the intelligence.

In Man the weight of	the	brain	is	to	the	body	as 1 to 36
„ Dog	„	„	„	„	1	„	305
„ Sheep	„	„	„	„	1	„	350
„ Horse	„	„	„	„	1	„	400
„ Elephant	„	„	„	„	1	„	500
„ Ox	„	„	„	„	1	„	860

(Colin.)

This rule is not absolutely true. There is considerable difference between the intelligence of a dog and a sheep. A horse is nothing like so intelligent as an elephant, and he is certainly not twice as intelligent as an ox. Personally I hold a very low opinion of the intelligence of a horse. The height of his intellect is exhibited when his stomach is his consideration. He takes an interest in the chase and race, but place him in a position of danger, or under any circumstance requiring the use of reasoning powers, and he is not only useless, but often a dangerous lunatic. He possesses, however, an excellent memory.

The cerebrum is composed of grey and white matter, the grey externally placed and thrown into convolutions. These convolutions in the lower animals, at any rate the horse, though well marked, are by no means regular in their position or direction, thereby forming a great contrast to the brain of man. The use of the convolutions is no doubt to increase the surface of the brain, and the deeper and more complex they are, the greater the intelligence of the animal. In the horse the convolutions are comparatively very shallow.

Motor Areas.—Until within a few years ago, the functions assigned to the cerebrum were simply those of intelligence and all the higher faculties; but experiment has shown that the grey matter of the cortex of certain convolutions,

forms the motor areas for certain groups of muscles on the opposite side of the body. By irritating these areas convulsions are produced, and by observation it is found possible to distinguish areas for the eyelids, face, mouth, tongue, tail, flexion and extension of the limbs, and many others. For veterinary purposes, especially dealing as we have done almost exclusively with herbivora, a knowledge of these motor centres is not required, nor have the exact positions of them been determined. We are content to know of their existence, but to the human surgeon they have opened up a new field of surgery, and one which promises the most important results.

After removal of the cerebral hemispheres all consciousness is lost, but muscular movements and equilibrium are retained. The cerebrum is insensitive to pain, but the dura mater is highly sensitive.

Besides the motor centres, sensory centres in the brain have been described, such as a visual, auditory, olfactory, taste, and tactile centres. A heat centre has also been described, stimulation of which produces a rise in temperature. The definite existence of these centres has not been agreed upon.

The respective functions of the grey and white matter of the cerebrum may be stated as follows: The grey matter is the seat of intelligence and the higher faculties; to the cells of the grey matter run the sensory fibres, both special and general; from the grey matter proceed the motor fibres supplying the voluntary muscles; the white matter is simply the conducting area, whereby the impressions made upon or issuing from the grey substance are distributed. The fibres of the white matter are arranged in a complicated manner, but ascending, descending, and transverse fibres have been recognised.

It has been supposed that the majority of the sensory impressions are implanted on the posterior half of the cerebrum; while from the middle and lateral portions arise the motor impulses; and from the anterior portion consciousness and intelligence.

Colin draws attention to the difficulty in producing paralysis experimentally in the horse from lesions of the hemispheres. Neither the artificial production of a clot in the falciform sinus, nor the introduction of pieces of lead the size of a pea into the convolutions, gave rise to hemiplegia. This quite bears out what we know to be a clinical fact, that horses may have in their lateral ventricles tumours the size of an egg without producing any disturbance. I have seen many such cases, the tumours being of variable size, and the clinical history has never given more than a few days' illness, though the growths must have been forming for a considerable period.

The circulation in the brain is peculiar. The veins, or so-called sinuses, are enclosed in very rigid membranous walls, the blood being driven through them, not only by the force behind, but by the aspiratory effect produced by inspiration (see p. 74).

The fluid found in the ventricles is a secretion rather than a transudation. The cavity of the ventricles communicates, by means of a foramen in the roof of the fourth ventricle, with the central canal of the spinal cord. The amount of fluid in the ventricles is normally 80 grains to 90 grains, but in disease may be as much as 7 ozs. to 10 ozs., according to Colin, who examined the brain of several horses suffering from *immobilité*, and says that in each case he found an excess of fluid in the ventricles.

For the peculiarities in the cerebral circulation, and the use of the cerebro-spinal fluid, see p. 73.

Nothing is known of the lymphatics of the brain.

Cranial Nerves.

These are divided into the nerves of special sense, sensory nerves, motor nerves, mixed nerves. Altogether they make twelve pairs, and all but Nos. 1, 2 and 3 arise from the medulla.

For nerves Nos. 1 and 2 see the Senses.

Third Pair, or Motor Oculi, is one of the motor nerves of

the eyeball; it supplies with motor power all the muscles (excepting the external rectus and the superior oblique), also the muscle of the upper lid. Through its connection with the lenticular ganglion it supplies fibres to the iris and ciliary muscle; it is also connected at its origin with two other motor nerves of the eyeball, viz., the fourth and sixth pairs.

The deep-seated origin of the third pair is from the corpora quadrigemina and peduncles of the cerebrum. Division of the nerve causes the eye to turn the temporal side of the pupil upwards and outwards, owing to the unbalanced action of the superior oblique and external rectus; there is also depression of the upper lid, immobility of the eyeball, and dilatation of the pupil. The action of the third pair will be discussed again in connection with the physiology of sight.

Fourth Pair, or Pathetic.—The motor nerve of the superior oblique muscle of the eyeball; it has a deep-seated origin in the valve of Vieussens.

Fifth Pair, or Pars Trigemini, resembles a spinal nerve in having two roots, a motor and sensory; and the resemblance is carried still further by the sensory root having a large ganglion on it, the so-called Gasserian. The motor root arises from the trigeminal nucleus, and is connected with the cerebral cortex on the opposite side. The sensory fibres arise from the sensory trigeminal nucleus; but fibres in connection with the origin of this branch can be traced upwards into the cerebrum and cerebellum, and downwards into the grey matter of the cord; further, it has also connections with all the nerves arising from the medulla, excepting the abducens. In this way can be explained the extensive connections and varied reflex acts of the fifth pair.

The motor branches, or inferior maxillary division of the fifth, supply the whole of the muscles concerned in mastication; by some it is considered that sensory fibres also exist in this branch.

The sensory branch, or superior maxillary division,

supplies the skin of the head, face, and anterior two-thirds of the tongue with ordinary sensation; it supplies the muscles of the face and jaw with sensation; it is the efferent nerve through which many important reflex acts are produced, and it acts as a trophic or nutrient nerve to many parts, such as the eye.

Division of the superior maxillary division of the fifth in the horse (Bell's experiment) prevents the animal from grasping food with its lips; not for the reason that they are deprived of motion, but owing to loss of sensibility the animal is unaware of how to take hold of the food; the relation of the fifth to muscular movements is that it keeps the muscles aware of the position of objects. As an afferent nerve in reflex acts it is most important; without it there could be no closure of the eye, nor sneezing; irritation of the conjunctiva would produce no tears, and no saliva, or but little, would be secreted. By division of its branches nutrition, taste, smell, and sight are affected. The cornea becomes opaque and sloughs, not merely because it is exposed to injury through the loss of reflex acts, but because the fifth pair controls its nutrition.

The fifth pair supplies the vaso-motor fibres for the bloodvessels of the eye.

Sixth Pair, or Abducens, arises from the floor of the fourth ventricle, and supplies the external rectus muscle of the eye with motor power. Paralysis of this muscle causes internal squint.

Seventh Pair (Portio Dura), or Facial, arises from the floor of the fourth ventricle. At its origin it is exclusively motor, but immediately afterwards becomes sensory and motor, through connection with the fifth, pneumogastric, and glosso-pharyngeal. The facial consists of two roots, one in the auditory nerve, the other the facial proper. The branches of the facial nerve are the petrosal, supplying motor fibres to the spheno-palatine ganglion, branches to the otic ganglion, and motor fibres to the tensor palati, tensor tympani, parotid gland, and the stapedius muscle of the internal ear. The important chorda tympani passes through

the middle ear, emerges and supplies the submaxillary gland with sensory fibres derived from the fifth, and secretory and vaso-dilator fibres (see p. 105). The chorda also possesses taste fibres for the margin and tip of the tongue, which it reaches through the lingual; these taste fibres are probably derived from the glosso-pharyngeal.

The other branches of the facial are distributed as motor fibres to the muscles of the face (those of expression, not of mastication), also to the muscles of the ear.

Division of the seventh nerve leads to alterations in sight, taste, hearing, smell, and facial expression. As it supplies the muscle which closes the eyelids, the orbicularis palpebrarum, conjunctivitis occurs from exposure of the eyeball; hearing is affected owing to paralysis of the muscles of the internal ear; smell is impaired owing to the paralysed condition of the nostrils; taste is affected through paralysis of the chorda.

The expression of unilateral facial paralysis in the horse is characteristic; the upper lip drawn to one side, the elongated nostril, the pendulous lower lip, escape of saliva and food from the mouth, the vacant look and the drooping ear, point clearly to the extensive distribution of this nerve.

Eighth Pair, or Portio Mollis.—Arises by two roots: one the nerve for the special sense of hearing, the other distributed to the semicircular canals, and assists through these in maintaining the equilibrium of the body (see 'Cerebellum').

Injury to the semicircular canals produces giddiness, not deafness, and certain movements (termed 'pendulum-like') of the head occur; the direction in which these are made depends on the direction in which the canals have been injured.

Ninth Pair, or Glosso-Pharyngeal, is a mixed nerve, though at its origin it is described as a sensory one. It supplies motor power to the muscles of the pharynx, and sensory fibres to the posterior third of the tongue, soft palate, part of pharynx, and anterior surface of the epiglottis. It is also a special nerve of taste, supplying the posterior third of the

tongue, and having special nerve-endings, known as 'taste-bulbs,' in the circumvallate papilla (see 'Taste').

Tenth Pair, or Pneumogastric.—This is both a sensory and motor nerve. At its origin it is intimately mixed up with the ninth, eleventh, and twelfth pairs of nerves, and later on with the sympathetic. It is the most extensively distributed nerve in the body, supplying respiration, heart, and digestive systems.

The sensory branches of the nerve are not highly endowed with sensation, probably for the reason that their chief function as sensory nerves is as afferent channels for reflex action. The motor fibres are joined by some from the spinal accessory, facial, and lingual.

The various branches of the vagus may be best studied by taking them in the order in which they are given off. The pharyngeal branch, through the pharyngeal plexus, supplies motor power to the pharynx (and in the horse supplies the cervical portion of the œsophagus with motor power), derived, it is said, from the spinal accessory nerve. The superior laryngeal furnishes the interior of the larynx with sensibility. The external laryngeal supplies motor fibres to the crico-thyroid muscle, the lower constrictor of the pharynx, and in a minor degree the anterior portion of the œsophagus. In the horse the crico-thyroid muscle is supplied by the first cervical nerve (see 'Voice'). The inferior, or recurrent, laryngeal is given off from the main trunk within the chest, on the left side winding around the aorta from without inwards, and on the right side passing around the dorso-cervical artery; both branches return up the neck and supply all the muscles of the larynx (excepting the crico-thyroid) with motor power. The branches are of great practical interest, inasmuch as they are affected (especially the left) in that common form of disease in horses known as 'roaring,' which is generally due to paralysis and atrophy of the muscles which dilate the laryngeal opening. After division of the recurrent nerves death by asphyxia is likely to follow. I have observed complete bilateral paralysis of the larynx in horses without asphyxia being

produced. The inferior laryngeal gives motor branches to the œsophagus and part of the pharynx, and exercises a controlling or inhibitory action over the respiratory centre. The cardiac branches of the vagus contain the inhibitory fibres of the heart, so that division of the nerve causes the heart to beat more quickly and with increased strength. The depressor nerve in rabbits is given off by the superior laryngeal; it is an afferent nerve of the heart; if irritated, and one vagus be intact, it slackens the heart, but only reflexly through the cardio-inhibitory centre; further it dilates the arteries, and causes a fall in blood pressure (see p. 72). The pulmonary branches supply both sensory and motor branches to the trachea, and motor fibres to the bronchi; they transmit to the medulla impressions which stimulate the respiratory and vaso-motor centres, causing through the latter a fall in blood pressure. Division of both pneumogastrics causes the breathing to become deeper and more prolonged, but does not produce a sense of suffocation; further, it causes the lungs to become gorged with blood, and produces a low form of pneumonia. The œsophageal branches supply the cardiac end of the œsophagus with motor power, the cervical portion of the tube being supplied by the pharyngeal branches; division of them causes the food to accumulate in the lower end of the tube. The gastric plexus supplies branches to the œsophagus, stomach, and liver. According to Colin's experiment on horses, division of both vagi does not influence either the secretion of gastric juice or the process of digestion, but owing to the paralysis of the lower end of the œsophagus, food is likely to accumulate in the stomach, œsophagus, and pharynx.*

The functions of the vagus may be summarised as follows: The vagus supplies (1) motor influences to the pharynx, œsophagus, stomach and small intestines, the larynx, trachea, bronchi, and lungs; (2) sensory and in part (3) vaso-motor influences to the same regions; (4) inhibitory influence to the heart; (5) inhibitory afferent

* I have to acknowledge Chauveau's experiments on the Vagus of the horse, published in the *Edinburgh Veterinary Review*, 1864.

impulses to the vaso-motor centre; (6) excito-secretory to the salivary glands; (7) excito-motor in coughing and vomiting (Kirke).

Eleventh Pair, or Spinal Accessory, arises by two roots: one from low down the cervical portion of the cord, the other from the medulla. It is essentially a motor nerve, but through being intimately connected with the pneumogastric it also possesses sensory fibres. The use of this nerve is to supply motor power to the sterno-maxillaris, trapezius, and a portion of the levator humeri muscles. It is supposed also to possess an influence over the larynx. Division of it produces no difficulty in breathing, as in the case of the recurrent laryngeal, but it causes loss of voice.

Twelfth Pair, or Lingual, arises in the lower animals by two roots, a sensory and a motor, the sensory having a ganglion on it. Both roots freely communicate with the pneumogastric, gustatory, and sympathetic. The branches of this nerve supply the tongue with motor power, and fibres to the muscles which depress the larynx.

The Sympathetic System.

Passing beneath the vertebræ from the cranium to the coccyx is a long chain of nerves, one on either side, composed of grey nervous tissue, and possessing on them at regular intervals a number of swellings or ganglia: these are the two main trunks of the sympathetic system. This remarkable system has free communication with all the cranial nerves (excepting the first, second, and eighth), and with the spinal nerves; the connection may be direct or through ganglia. It is composed of two systems of fibres: the grey fibres which possess no white substance of Schwann, and the medullated or ordinary cerebro-spinal fibres, the latter being remarkable for their fineness, and derived from both the superior and inferior roots of the spinal nerves. By passing through the ganglia the medullated become non-medullated fibres.

The characteristic feature of the sympathetic system is

the extensive ganglion connections by which it is brought into communication with the cranial and spinal nerves.

Gaskell has shown that these communications may be classified as follows: (1) The long chain on either side of the vertebræ, termed by him the 'vertebral' or 'lateral ganglia'; (2) in connection with these and with each other are the large nervous plexuses of the chest and abdomen, such as the mesenteric, solar, etc., and these he terms the 'collateral ganglia'; (3) ganglia situated in the substance of organs, known as 'terminal ganglia,' and which are in connection with the collateral ganglia (Fig. 24).

Each spinal nerve is connected by fibres proceeding from the superior and inferior roots, with the ganglia on the vertebral portion of the sympathetic system. By this remarkable chain of communication, the entire nervous system is able to work as one harmonious whole.

One of the most important functions of the sympathetic, is the influence exercised over the bloodvessels by means of the vaso-motor system of nerves.

Vaso-motor nerves are of two kinds: 1. Vaso-constrictor. 2. Vaso-dilator. Both fibres arise in the brain or spinal cord, but possess well-marked differences.

The vaso-constrictor arise in the middle region of the cord, viz., from the second dorsal to the second lumbar; running out with the inferior spinal nerve they reach, by means of the ramus communicans, the gangliated cord of the sympathetic (running beneath the arches of the ribs); from here some pass forward to the head and neck, others to the fore-leg, others to the thoracic and abdominal viscera, and, lastly, others to the hind-leg; they reach their various destinations either directly through the sympathetic system, or through recurrent branches of the sympathetic (grey ramus communicans), which join the cerebro-spinal nerves of the fore and hind legs and trunk. It is to be noted that the constrictor fibres, after passing through the ganglia found on the cord of the sympathetic, have, from being medullated, now become non-medullated fibres.

It is believed that the vaso-constrictor fibres are con-

stantly in a state of moderate activity, by which the general arterial tone of the body is preserved; this forms a contrast to the dilator fibres, which are only active occasionally.

If now we look at the vaso-dilator fibres we find that they behave differently; their origin from the cord is by no means well known, but there is reason to believe that they run in the roots of the motor-nerves to their destination, and do not pass through the sympathetic system as we have found the constrictor fibres to do; moreover, they retain their medulla until near their termination.

The constrictor fibres of the whole body are under the control of a constrictor centre in the medulla known as the vaso-motor, though under certain circumstances independent centres may exist in the spinal cord.

The dilator fibres are believed to have no special centre in the central nervous system, but are affected by whatever changes influence the centres of the motor-fibres they accompany.

If the vaso-constrictor nerves be divided, the vessels become relaxed through the unbalanced action of the vaso-dilators, and a considerable quantity of blood is sent to the part. If the vaso-constrictor nerves be stimulated, the vessels under its influence contract and press the blood onwards, thus relieving the physiological congestion. No better example of this can be found than in the nervous supply of the submaxillary gland: the chorda tympani contains fibres which act as vaso-dilators; if the chorda be stimulated, the vessels of the submaxillary gland dilate and the veins pulsate; if now the sympathetic be stimulated, the vessels contract and the blood stream slows down—the sympathetic therefore acts as a vaso-constrictor apparatus.

Visceral Muscle Supply.—The next important function of the sympathetic is the supply of nerve force to the involuntary muscular fibres of the body: in this way the peristaltic movements of the stomach and bowels are maintained. These movements are independent of the brain and spinal cord, and are maintained by local ganglia.

The fibres supplying the visceral muscles with motor power arise from the cervical portion of the cord, and exert their function through the vagus nerve. The viscero-motor nerves are in turn controlled by viscero-inhibitory; these pass from the inferior roots of the spinal nerves, direct to the tissues through the abdominal splanchnics; they are, therefore, not connected with the vertebral ganglia.

It is probable that all the glands of the body are supplied with sympathetic fibres, in the same way as has been demonstrated to occur in the submaxillary gland.

Sympathetic Ganglia.—We have before noticed that when medullated nerves pass through a sympathetic ganglion, they lose the white substance of Schwann and become non-medullated; they also become more numerous, for nerve fibres originate in the ganglia, arising from the ganglion cells found in this structure. It is not known whether the sympathetic ganglia possess the same properties as the cerebro-spinal ganglia.

Trophic Influences.—Sympathetic ganglia also exercise through the nerves leaving them, a trophic or nutritive influence over parts. Gaskell's views in connection with this matter are most important. He considers that every tissue has nerves which excite repair, and are termed anabolic, and others which excite waste, and are termed katabolic. We mentioned this theory in connection with the heart, the sympathetic nerves of which excite katabolism by increasing the heart's action, whilst the pneumogastric exercises processes of repair, its function being to control the heart: it is therefore regarded as an anabolic nerve.

Sweating is produced through the vaso-motor fibres of the sympathetic, in conjunction with the secretory nerves: section of the cervical sympathetic in the horse leads to sweating on that side of the neck and head (see p. 195).

For the effect on the secretion of saliva by division of the sympathetic, see p. 106.

CHAPTER XVI.

THE SENSES.

Sight.

The delicate structures composing the eye receive a very thorough protection by the anatomical arrangement of the parts. The orbital cavity, for example, is nearly entirely surrounded by bony walls, and layers of fat within it assist the muscles in protecting the globe and the optic nerve; the eyelids sweep the cornea and protect the part from dust; the tears keep the face of the cornea brilliant; the membrana nictitans removes particles of solid matter which would otherwise produce injury; the eyeball can also be retracted to a considerable extent to further assist it in withdrawing from injury. The size of the orbit is such that ordinary blows inflicted upon the eye are expended on the margin of the orbital cavity, and not on the eyeball itself; so that the risk of injury to this delicate part arises less from large than from small bodies.

The arrangement of the eye corresponds very closely with that of a certain well-known physical apparatus the camera, where into a dark chamber is thrown the inverted image of an object, the inversion being produced by a double convex lens placed in front: the amount of illumination being regulated by a diaphragm, and the focussing power also capable of adjustment.

The eye is composed of a convex surface in front, forming a chamber containing fluid, immediately behind which is the iris or diaphragm, through which the light passes into a biconvex lens; issuing from the posterior surface of the

lens, the light passes again through a fluid medium, and comes to a focus on a delicate expansion of nerve tissue, which takes a reduced and inverted impression of the picture presented. The physical arrangement of the camera and the eye are, therefore, practically identical.

The shape of the eyeball is spherical, its vertical being somewhat longer than its transverse axis; the optic nerve penetrates it close to the floor, and inclined to the temporal side of the eyeball.

The optic nerve has a deep-seated origin in the optic thalamus, corpora geniculata externum and internum, and corpora quadrigemina; these unite on the base of the brain to form the optic nerves, which decussate in the well-known manner. This decussation, so productive of sympathetic ophthalmia in man, never, in my experience, gives rise to sympathetic ophthalmia in the horse. The nerve runs in the substance of the retractor muscle, and makes a distinct dip downwards before penetrating the globe.

By means of the optic nerve the impulses due to the action of light on the retina are conveyed to the brain; the optic nerve conveys nothing else but luminous impulses; stimulation of the nerve causes flashes of light, but no pain; division of the nerve is therefore painless, but the sheath of the nerve causes pain when cut. The optic nerve, by its expansion the retina, collects the impulses due to the action of light, which are then referred to the brain by means of the nerve itself. The natural stimulus of the retina is light; we must therefore briefly study the changes occurring in the rays of light while passing through the various refracting media of the eye, which result in the formation of images on the retina.

A beam of light is said to consist of a number of rays, each ray running parallel to its fellow, and continuing in this position unless it meets with a body which turns it back in nearly the opposite direction to which it has been travelling, viz., reflects it, or with a body which will allow it to pass, but only on condition that the parallel rays become bent. This bending is termed **refraction**.

A ray of light passing from a rarer to a denser medium becomes refracted; it does not matter whether this medium be water, glass, or diamond, a greater or less bending of the ray occurs.

A ray of light passing through a convex lens also becomes refracted, but before we can follow exactly how this refraction occurs, it is necessary that we should be acquainted with the various parts of a lens.

A convex lens has two curved surfaces, and a line drawn through the centre of these two surfaces is known as the

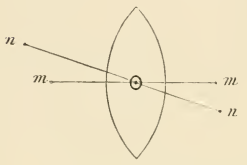


Fig. 27.

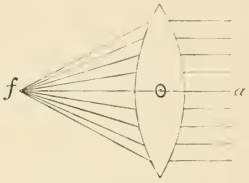


Fig. 28.

Figures illustrating the Action of Lenses upon Rays of Light passing through them.

Fig. 27.—Biconvex lens; O, optical centre; *m*, *m*, chief axis; *n*, *n*, chief or principal rays.

Fig. 28.—Rays falling upon a lens parallel with the principal axis *a*, *f*, are so refracted that they are collected on the other side of the lens at a point called the principal focus *f*; the distance from O, the optical centre, to *f*, is called the focal distance of the lens. The converse of this condition is also true, viz., rays which diverge from a focus pass through the lens, being on the other side parallel with the principal axis without coming together (Landois and Stirling).

principal axis of the lens. The essential idea of a double convex lens, is that it is thicker at the centre than at the edges.

Situated on the principal axis of a biconvex lens at a point in its interior is the **optical centre** (Fig. 27); any straight line passing through the optical centre is termed **a secondary axis.**

Parallel rays of light passing through a convex lens, are refracted or bent in such a way that they collect on the

opposite side of the lens at a point termed the focus; every ray passing through the lens is refracted, excepting those passing through the optical centre (see Fig. 28). If instead of the rays being parallel, they diverge from a luminous point, and that point be the focus, and pass through a convex lens, then by passing through, they are rendered parallel (Fig. 28).

If rays of light be passed through a convex lens *from a point beyond* its focus, after passing through the lens, and so becoming refracted, they meet again instead of becoming parallel, and the rays cross at some point, in such a manner that the upper ray becomes the lower one, and the lower ray the upper one; in other words, the image formed under these conditions is inverted (see Fig. 29).

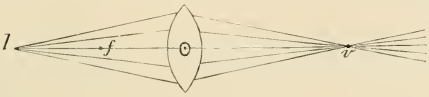


Fig. 29.

Rays of light passing through a convex lens from *l*, at a point beyond the focus *f*, cross at some point *r*, and invert the image (Landois and Stirling).

Applying these physical conditions to the eye, we find that the rays of light passing into and through the cornea are refracted; they are further refracted passing through the aqueous humour, considerably refracted passing through the dense substance of the lens and vitreous humour, and brought to a focus on the retina in such a way that the retinal picture is upside down, and is only a miniature though perfect representation of the object presented to the eye (see Fig. 30).

The rays of light passing from X Y (Fig. 30) are refracted and cross in the lens; those rays, such as a and a′, pass through the lens without refraction, as they pass through its optical centre; the further behaviour of the rays is shown in the diagram, and the method by which the inversion of the picture is produced. The angle

X n Y is spoken of as the **visual angle**, and it is equal to the angle Y n X. All objects having the same visual angle form the same sized picture on the retina, whether they be near or far.

The retinal image though inverted, is mentally referred not to the retina, but to the direction from which it has proceeded. Thus to the mind of the animal the picture is not seen at Y A X, but referred to X O Y.

The **optical axis** of the eye is the straight line through the eye which passes through the centre of the refracting media.

The eye is liable to certain defects in its refracting media, due either to its shape or errors in the curvature of the refracting surfaces.

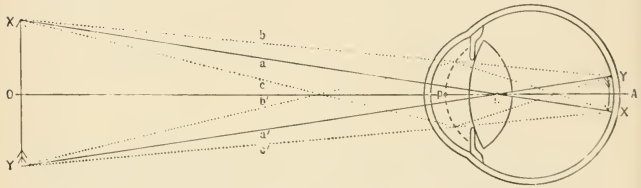


Fig. 30.—Diagram of the Formation of a Retinal Image (Foster).

a, principal ray of the pencil of light proceeding from X; a′, principal ray of the pencil of light proceeding from Y; the principal rays pass through the eye without being refracted; the other rays b, c and b′, c′ are refracted. In this way the arrow X O Y forms a smaller inverted image of an arrow on the retina Y A X.

Spherical Aberration.—The rays of light passing through a convex lens are not all equally refracted, the rays passing through the circumference being more bent than any others; if the rays be derived from an object situated at the side of the field of vision they do not all meet in the same point, those passing through the circumference of the lens coming to a focus earlier than those passing through the centre. This defect, known as 'spherical aberration,' is remedied in the eye by the introduction of a diaphragm or iris, which prevents some of the rays of light from passing through the circumference of the lens.

Spherical aberration produces indistinctness of vision by the production of circles of diffusion, caused by those rays which met too early crossing each other and forming a circle.

Chromatic Aberration is due to the decomposition of white light into its primary colours—viz., the formation of a spectrum—by passing through a prism or a convex lens. The colours of the spectrum are differently refracted, the red being the least bent, the violet the most; when therefore we can see the red distinctly the eye is not focussed for the violet. Chromatic aberration is prevented in the eye by the unequal refractive power of the various media.

Astigmatism is due to irregularities in the curvatures of the cornea. The curvature of the vertical meridian is frequently greater than that of the horizontal meridian; by this difference in the curvatures of the refracting surfaces whether lens or cornea, but generally the latter, the rays of light cannot be focussed in one point, but in two different focal points, of which the focus of rays falling on the vertical meridian, lies in front of that for the rays of a horizontal plane.

Emmetropia.—We shall presently have to speak of accommodation, or the means by which the eye is focussed; but it is necessary here that we should understand that by the term 'range of accommodation' is understood the power the eye possesses of seeing distant objects 'as far as the eye can reach,' and also of seeing near objects distinctly up to 8 inches. Between 8 inches and infinity parallel rays of light should still be focussed on the retina so as to form a distinct image; such an eye is termed emmetropic.

But all eyes do not possess this range of vision; some are perfect for close objects, others are only perfect for distant ones. The one eye is short-sighted, the other long-sighted; the explanation of these two conditions lies in the shape of the eyeball.

Myopia, or short-sightedness, is due to the eyeball being too long, whereby the focal points of the image, instead of

being thrown upon the retina fall in front of it, the rays crossing and forming a diffused circle on the retina. If in Fig. 31 the retina lies at G—viz., the eyeball is too long—the rays of light will focus in front of it and diverge at *a* and *b*.

Hypermetropia, or long sight, is due to the opposite condition—viz., the eyeball being too short—whereby the rays of light are focussed behind the retina instead of on it. The retina of a hypermetropic eye would be situated at H (Fig. 31); the rays of light at *e* and *f* have not yet come to a focus. In this condition, by a great effort of accom-

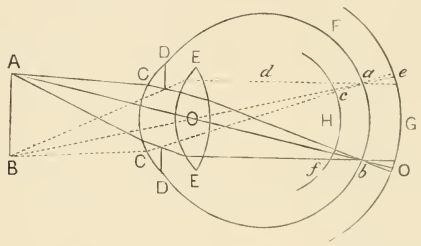


Fig. 31.—Diagram to illustrate Myopia and Hypermetropia. G, the position of the retina in a myopic eye, a blurred image from A B is perceived at *e* and *o* which are beyond the focus: H. the position of the retina in a hypermetropic eye, the image from A B is blurred at *e f*, which are in front of the focus; F, the position of the retina in the emmetropic eye, the rays from A B are brought to an exact focus at *a b* (Kirke).

modation (a term which will be presently explained), the divergent rays from a near object may be caused to focus on the retina; the parallel rays from distant objects are generally well seen without any great effort of accommodation.

Since myopia and hypermetropia are due to the rays being brought to a focus either in front of or behind the retina, if we could supply horses with convex or concave spectacles, their myopic or hypermetropic condition would be of no serious disadvantage.

In the normal eye the retina must be situated the proper

focal distance from the lens; if too close long sight results, if too far away short sight is produced.

Accommodation.—We must now consider the question of accommodation, and the manner by which it is brought about.

The near point of the eye lies at about 8 inches from it; the far point in the emmetropic eye is infinity. It is not necessary, however, that the eye should be capable of focussing, adjusting, or accommodating itself for any and every range between 8 inches and infinity, for at a point a little over 200 yards from the eye the rays of light for all

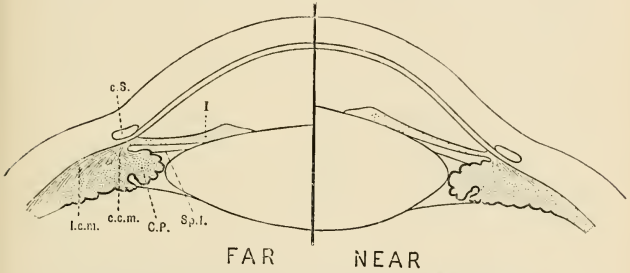


FIG. 32.—DIAGRAM TO ILLUSTRATE ACCOMMODATION.

C.P., ciliary process; I, iris; Sp.l., suspensory ligament; l.c.m., longitudinal ciliary muscle; c.c.m., circular ciliary muscle; c.S., canal of Schlemm (Foster after Helmholtz).

The left half represents the shape of the lens for viewing far objects, and the right half that for viewing near objects.

practical purposes are parallel, and no effort of accommodation is required. From 8 inches up to 200 yards the eye has to be capable of focussing itself, and the mechanism by which this is produced we will now study.

The rays of light passing through a convex lens, will be brought to a focus at a greater or less distance behind the lens, depending upon its curvature; thus, the thicker the lens the shorter the focal length, and *vice versâ*. It is obvious, therefore, that any mechanism which can alter the curvature of the crystalline lens of the eye, will adjust it for distant or near vision; such an arrangement exists. The

crystalline lens may be made flatter or more convex, and the process which brings this about is termed the 'mechanism of accommodation.'

The crystalline lens is contained within a capsule; to this capsule is attached the zonula ciliaris, which in turn is attached to the choroid. So long as the zonula is tense the lens is flattened; but if the tension be removed, the natural elasticity of the lens causes it to bulge forward and become more convex. The tension of the zonula is removed from the lens by means of the ciliary muscle, which draws forward the choroid coat, relaxes the zonula, and the lens becomes convex. In this way the accommodation of the eye is adjusted (Fig. 32).

Whilst on this point mention may be made of the reflec-

Fig. 33.—Diagram of the Katoptric Test.

A, from the anterior surface of the cornea; B, from the anterior face of the lens; and C, from the posterior face of the lens.

tions obtained when examining the eye with a candle—the so-called **katoptric** test. When a candle is held opposite the eye three images of the flame are seen: one a very sharp bright one, obviously reflected from the cornea; a second much duller, but also large, reflected from the anterior surface of the lens; and a third very small, brighter than the middle one, and *inverted,* reflected from the posterior part of the lens. In a normal eye these are seen perfectly, and move in a definite direction when the candle is moved, the inverted one in an opposite direction to the two erect images, and all are equally visible at any surface of the lens* (see

* The blurring or duplicature of the images, especially the second one, is a good ordinary test for opacities of the lens.

Fig. 33). The eye all this time we must suppose to have its accommodation relaxed, and to be looking into distant space; if now it be focussed on a near object, the lens becomes convex, and the second image of the candle advances and it becomes smaller and clearer.

At the moment when the ciliary muscle acts the pupil contracts, and when the muscle is relaxed it dilates. This is due not only to the intimate connection existing between the ciliary muscle and the iris, but also both are supplied by the same nerve—viz., the third cranial.

The **Iris**, or diaphragm, performs the same function as a shutter: it regulates the amount of light entering the eye, and, as pointed out in speaking of spherical aberration, it cuts off those rays entering at the circumference of the lens, and so introduces a correction for spherical aberration.

The movements of the iris are brought about by two sets of muscles—a sphincter and a dilator (?). The former surrounds the pupil, and by contracting closes it; it is supplied with nervous power through the third pair. The dilator by contracting opens the pupil, and its nervous supply is furnished chiefly by the sympathetic. The existence of a dilator muscle, though very probable, is not absolutely proved; but it is certain that the contraction of the pupil is under the control of the third pair of nerves, whilst its dilatation is produced by the sympathetic.

The ordinary contraction of the pupil due to light is a well-marked reflex action.

The iris would also appear to be affected by the action of light. In a horse, for instance, just destroyed, the pupil dilates considerably, and yet in a few hours' time it has undergone extensive contraction. It is said that if the eyes remain covered up the subsequent contraction does not occur. It is important to note that the pupil of the horse *dilates* under artificial light, a point to be referred to presently.

The opening in the iris—termed 'the pupil'—is elliptical in herbivora. The range of movement is extensive, from a mere ring of iris, such as may be obtained under atropine,

to a simple slit of pupil, such as is seen in sunlight; in fact, owing to the presence on the edge of the iris of some large pigmentary bodies, which completely block up the centre of a powerfully contracted pupil, it is wonderful how sufficient light finds its way into the retina during sunlight.

The function of these black bodies (which are sometimes so large as to cause serious apprehension about the vision) is obscure; that they assist in absorbing rays of light appears certain, but their position in the centre of the pupillary opening would certainly not be the most suitable position for a light-absorbing substance, and therefore they must have some other function. We believe that they may assist in rendering vision binocular when both eyes are turned to the front; but this point will be touched upon later. It only remains here to note that the horse appears to be the only animal possessing them.

The colour of the iris is brown in the horse, occasionally bluish white, as in 'wall-eyed' horses. It is of a brighter brown in the ox, and is of a brownish yellow in the sheep.

The Retina.—The expansion of the optic nerve within the eye is termed the retina; it is a thin, delicate membrane, covered by the vitreous humour in front and the choroid behind. Microscopically, it consists of several layers, of which the so-called rods and cones is the most important, for the reason that the cones are the parts most concerned in vision. The entrance of the optic nerve is a good example of this; there are neither rods nor cones over the optic nerve at its entrance, and in consequence the part is quite blind. There is no yellow spot or area of intense vision in the horse or other herbivora; it is possible that the region of the tapetum is the area of the retina which is most excited by light.

The **Tapetum Lucidum** is part of the choroid coat; it is of a remarkably brilliant colour, being in the horse of a greenish yellow, and occupying a somewhat semi-lunar space above the optic nerve. It is formed of 'numerous undulating

bundles of connective tissue, giving a metallic lustre to the eye. The colour is not due to pigment, but is iridescence caused by interference of waves of light' (M'Kendrick). Over this region there is an entire absence of the pigment so characteristic of the inner surface of the choroid, and the appearance of the fundus of the horse when examined by the ophthalmoscope is an extremely beautiful object.

The Ophthalmoscope.—We may here describe in outline the theory of this instrument, and the appearance of the picture presented by it.

To examine the eye, a mirror with a hole in the centre is applied to the eye of the observer; from a suitable source of light rays are thrown through the pupil on to the retina to be examined.

When a light is thrown into the eye, the rays are reflected back through the pupil in the direction in which they entered, and pass through the hole in the mirror into the eye of the observer.

This is the principle of the ophthalmoscope. On looking through it at the retina of the horse, a remarkable golden-yellow or greenish-yellow surface is illuminated studded with minute dots; this is the tapetum. Examination shows this surface to be situated above the optic papilla, and to be half-moon in shape; below it the optic papilla comes out of a reddish or pink colour, with a slightly raised whitish margin. It is so difficult to study the eye, owing to its frequent movement, that only occasional glimpses of the papilla can be obtained. From the optic papilla several vessels may be seen radiating, but extending no great distance from it. This is characteristic of the retina of the horse. The remainder of the fundus is purple or brown, the shading in it resembling that employed for representing mountains in a map.

Owing to the presence of the tapetum in the horse, a perfect examination of the lens, and a fair examination of the fundus may be made without the aid of artificial light; under the influence of artificial light the pupil dilates so much that there is no need for the use of atropine.

As before noticed, there is no yellow spot in the eye of herbivora, and the tapetum is probably the area of the most acute vision.

In the rods of the rod and cone layer of the retina is a peculiar pigment known as the **visual purple**; it can be obtained from eyes kept in the dark, but in those exposed to light it rapidly becomes bleached, though it reappears when the light is again excluded.

Pictures have been printed on the retina through the aid of the visual purple; its exact use is not known, though the photographer's process is suggestive of its probable use. Unfortunately for this theory it is absent from the cones, which are known to be the instruments of the most acute vision.

Movements of the Eyeball.—We have now to consider the mechanism by which the eye is brought to bear on any desired point, and the subject is somewhat complicated by the fact that with most quadrupeds the eyes occupy a lateral position in the head, in such a way that in many cases vision is only one-eyed, and not two-eyed as in the human subject. Further, the chief movements of the head are not from side to side as with us, but up and down, and as the pupil remains horizontal, no matter what the position of the head, it is evident that rotation of the eyeball must occur. If it were not for this rotation the pupil in the uplifted head would be vertical instead of horizontal, and, in the depressed head, it would be obliquely instead of horizontally placed.

The muscles working the eyeball are seven in number: four recti, two oblique, and one retractor. The use of the recti is clear enough; they turn the eye in four directions, outwards, inwards, downwards, and upwards. The two oblique muscles rotate the eye in opposite directions; the superior oblique turns the nasal side of the pupil downwards, and the eye can rotate upwards until the pupil, with the head in the normal position, becomes vertical instead of horizontal; the inferior oblique turns the nasal side of the pupil upwards. The retractor pulls the eye

backwards into the socket. The following table shows the action of the ocular muscles:

Eye turned upwards and inwards ...	Sup. rectus, int. rectus, and inf. oblique.
Eye turned downwards and inwards ...	Inf. rectus, int. rectus, and inf. oblique.
Eye turned upwards and outwards ..	Sup. rectus, ext. rectus, and sup. oblique.
Eye turned downwards and outwards ...	Ext. rectus, inf. rectus, and sup. oblique.

When the head is elevated the superior oblique renders the pupil horizontal, when depressed the pupil is horizontally placed by the inferior oblique.

With the exception of the external, all the recti muscles, the inferior oblique, and the retractor, are supplied with nerves by the third pair; the fourth pair supplies the external rectus, and the sixth pair the superior oblique. The orbicularis palpebrarum, which closes the eye, is supplied by the seventh nerve, and the muscle which raises the upper lid derives its nerve supply from the third pair.

It will be observed that the muscles of the two eyes employed in any movement may be the corresponding muscles in both eyes or not; both eyeballs may, and commonly are, directed to the front, producing what would be known in man as a decided internal squint: in this case the same group of muscles in each orbit are employed; but if the left eye moves backwards, the right eye goes forwards, and *vice versâ*. Here the groups of muscles employed are different in each eye, for while the external rectus is acting on the left eye and drawing it back, the internal rectus is drawing the right eye forwards.*

Monocular and Binocular Vision.—When a horse looks direct to the front (Fig. 34), he is capable of seeing an object with both eyes; he produces a marked internal double squint, the eyes being rotated inwards and upwards by the combined action of the superior and internal rectus,

* The terms employed here of backwards and forwards, express the same condition as outwards and inwards when applied to ourselves.

and inferior oblique muscles, the object being to bring the pupillary opening as far as possible to the front. That the horse succeeds in this can be readily determined by simple inspection; the inner part of the iris, as far as the edge of the pupil, may often be seen in both eyes to disappear beneath the folds of the eyelid, in the powerful endeavour to concentrate both eyes on an object situated directly to

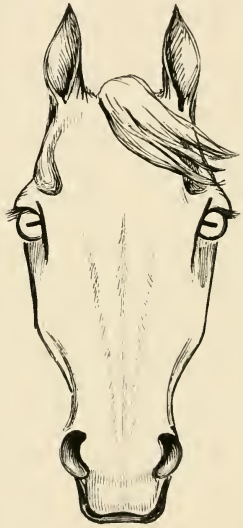


Fig. 34.—The Position of the Head and Eyes in Binocular Vision.

the front. In no other position has the horse binocular vision (that is to say, single vision resulting from the employment of a pair of eyes), and to direct the rays of light into the outer half of each lens, the corpora nigra appear to be placed in the centre of the pupillary opening.*

* The great argument which tells against this theory is that ruminants, which have also binocular vision, have no corpora nigra. Their

Whether this be the function of these black bodies or not, does not affect the accuracy of the statement that binocular vision in the horse can only occur when a powerful internal squint is produced, and the eyeballs directed well to the front. Monocular vision is otherwise the only one of which animals with their eyes situated on the lateral side of the head are capable, when from the position of the object both eyes cannot be directly concentrated upon it. Monocular vision would appear to be as perfect as binocular, though on this point it is difficult to speak with certainty. Though ordinary vision is monocular, yet the right eye will blink when an attempt is made to strike the left, though the left cannot possibly see what is going on.

In man binocular vision is perfect, and the explanation afforded is that any part of one retina corresponds to the same part of its fellow; so that if the retinæ be laid over one another, the left portion of one will lie exactly over the left portion of the other, and their right upper and lower parts will equally correspond. But the temporal side of one eye corresponds to the nasal side of the other. For instance, in Fig. 35, the two circles represent the two retinæ divided into quadrants, L being the left, and R the right eye; a and c in the left eye, correspond to a′ c′ in the right eye; and b and d in the left, correspond to b′ and d′ in the right eye.

When the two images of an object fall on corresponding points of the retina, then vision is binocular and only one object is seen; thus, if the rays fall on the right side of one retina, they must fall on the right side of its fellow; in Fig. 35 this is shown, v l from x to x′, and x to x are the two visual axes. If the centre x of an object be looked at the corresponding points which lie on the right side of one retina, lie on the right side of the other also, and conversely. Owing, then, to the manner in which the human

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eyeballs are so prominent that it is possible that here they are not needed.

eyes are placed in the head, and the convergence of axes of the eyeball, a ray of light from any point is imprinted upon the same part of the retina in both eyes, and we see it not as a double image, but as a single one.

This explanation does not apply to the horse or ox; no

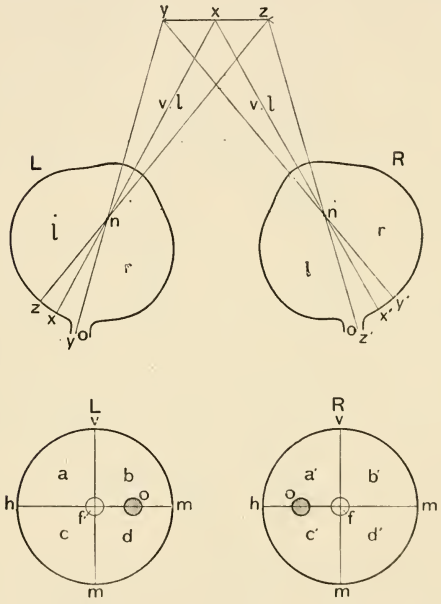

FIG. 35.—DIAGRAM ILLUSTRATING CORRESPONDING POINTS. (FOSTER.)

z′ x′ y′ are points in the right eye corresponding to z x y in the left eye; v l, visual axis. The two figures below illustrate the corresponding points on the retina, described in the text.

matter how greatly the eyes may be converged in order to see an object, the rays of light do not fall on the same side of the retina, but on *opposite sides* of it. The diagram (Fig. 36) will make this point clear.

The outer part or temporal side of the retina in the

horse, corresponds with the temporal side of the opposite eye; while the nasal side cannot correspond with the nasal side of the other eye, as it is not possible for a ray of light from an object to strike both nasal sides at one time (see Fig. 36).

Cartilago Nictitans.—The retractor muscle of the eye withdraws the eyeball within the orbit, and the pressure thus produced within the cavity forces the cartilago nictitans

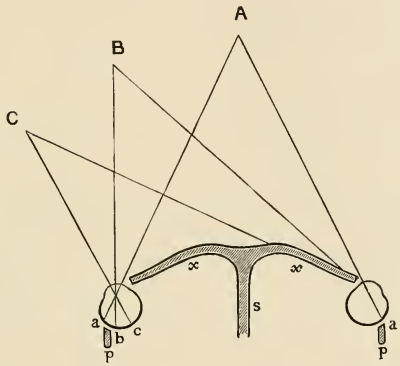

FIG. 36.—DIAGRAM OF HORIZONTAL SECTION OF THE HEAD PASSING THROUGH BOTH EYEBALLS, TO ILLUSTRATE CORRESPONDING POINTS IN THE RETINA OF THE HORSE.

x x, the frontal bones; p p, portion of malar bone entering into the formation of the outer rim of the orbit; s, the nasal septum. Rays of light proceeding from A are seen by both eyes, being imprinted on the temporal side of each retina at a; rays from B are seen at b in the left eye, but are not seen with the right eye. In the same way rays from C are imprinted at c in the left eye, but cannot be seen with the right eye.

forward to such an extent, that it may be made to sweep nearly the whole corneal surface.

The reason why the cartilage is pressed forwards is due to the fact that, naturally curved, it becomes flattened by the pressure caused by retraction, and shoots forward; when the pressure is removed it retires through its own elasticity, becoming curved once more.

On the cartilago of some animals is a small gland termed the Harderian; its use is to prepare an unctuous secretion, probably of a protective nature.

In the eyelids are found numerous glands, the Meibomian, which furnish an oily secretion, and prevent the overflow of tears.

The **Tears** are secreted by the lachrymal gland, placed on the upper surface of the eyeball; they find their way into the conjunctival sac by several small tubes. The use of the tears is to keep the cornea moist and polished, and to wash away foreign bodies. The tears find their way through the narrow puncta into the lachrymal sac, and so into the nostril; once in the sac the descent to the nostril is readily understood; but it is not clear why the tears prefer passing through a narrow slit in the eyelid to running over the side of the face; probably the only explanation is the unctuous secretion mentioned above.

The **Eyelashes** of the horse are peculiar. Those on the lower lid are very few and fine, whilst on the upper lid they are abundant, and exist not in one single row but a double one; the rows crossing each other like a trellis-work, but without interlacing; these eyelashes are very long and strong. A few protective hairs grow from the brow and below the lower eyelid; in some horses they are four or five inches in length. They appear to be in connection with nerve terminations, for their delicacy to the sense of touch is remarkable. They are doubtless protective, and give the eyes previous warning of danger.

Smell.

In order that the sense of smell may be obtained, it is necessary that a sensory surface specially endowed should exist, the connection of which by a nerve with the brain should be intact. The special nerve of smell is the olfactory, and the special smell centre in the brain is (according to Ferrier) in the tip of the uncinate gyrus, on the inner surface of the cerebral hemisphere. The olfactory bulbs are hollow in the horse, filled with fluid, and communicate

with the lateral ventricles. From the olfactory lobes is given off the olfactory nerves, which pass out through the cribriform plate of the ethmoid bone, and ramify over the middle meatus and superior turbinated bone. Owing to the fact that the olfactory nerve is not distributed over the entire area of the nasal chambers, it is usual to divide this cavity into two areas—an olfactory and a respiratory portion. The special nerves of smell ramify in the mucous membrane covering the parts named, but they have no special end organs. In appearance the olfactory, owing to the greyness of its fibres, resembles the sympathetic nervous system.

In all animals in which the sense of smell is acute the turbinated bones are remarkably convoluted; this is more marked in carnivora than in herbivora. There are certain substances which excite the olfactory organs more readily than others: thus, in carnivora, flesh, blood, or any animal matter, has a remarkably stimulating effect; in herbivora, plants, grasses, and vegetable products have a characteristic effect, while the odour of blood is evidently repulsive, and often causes nervousness and fright. Some of the herbivora have remarkably keen scent; antelopes and deer have the power of smelling the presence of man when even a considerable distance away. The sense of smell plays an important part in the sexual relations of animals, for the female in the 'rutting' period may be distinguished at a considerable distance.

The organ of Jacobson, which is well marked in herbivora, is said to have some connection with the sense of smell. Cuvier regarded it as the means by which the herbivora distinguished between poisonous and non-poisonous plants. This can hardly be correct; cattle poisoning is comparatively common.

Before a substance can be perceived by the olfactory nerves, it has to become dissolved in the mucous coating of the part—in fact, it is considered that substances can only be perceived by the sense of smell either in the form of a vapour or liquid, as the sense is nearly or entirely lost if the membrane be dry.

The odour of a body can be more certainly obtained by 'sniffing.' This is an inspiratory act, producing a rarefaction in the nasal chambers, which is overcome by more air rushing in to restore equilibrium: by this rushing in the air is forcibly brought into contact with the olfactory area. The sense of smell rapidly becomes blunted, the olfactories apparently get used to an odour; an unpleasant smell is always more offensive when first detected than it is a few minutes later.

In connection with the nasal chambers are the facial sinuses, which in horses and cattle are very extensive cavities filled with air, (which they derive from the nasal chambers), and lined by a mucous membrane derived from the Schneiderian. This membrane cannot distinguish smell, according to Colin's experiments, nor should we expect it to.

The use of these sinuses is to make the head larger without being heavier, and thus afford more surface attachment for the muscles. During health the membrane lining the cavities is moistened with a watery fluid; but under diseased processes, which are very frequent, the cavity becomes filled with pus.

By the sense of smell animals have the power of distinguishing good from bad, eatable from uneatable; and, moreover, through this sense sexual activity is excited.

Sensibility is supplied to the nasal chambers by the nasal branch of the fifth nerve, not by the olfactory.

Taste.

The special nerve of taste is the glosso-pharyngeal, and the portion of the mouth where the sense principally lies, though not fully agreed on by physiologists, is the root of the tongue and soft palate. The part of least taste, or no taste at all, is the dorsum of the tongue; this is due to the dense coating of epithelium.

The glosso-pharyngeal nerve consists of medullated and non-medullated fibres; the former terminate in end bulbs, the latter in taste goblets (M'Kendrick).

The taste goblets are balloon-shaped bodies, found principally in the circumvallate papillæ; in the top of the balloon or goblet is a depression or funnel, termed a 'taste-pore.'

With reference to the position of these taste goblets in the lower animals, M'Kendrick gives the following details: The taste goblets appear principally on the side of the circumvallate papillæ—1,760 taste goblets were counted in a papilla of the ox; in the papilla foliata of the sheep 9,500 goblets, and in the ox as many as 30,000 goblets have been observed. There can be no doubt that taste is due to these bodies acting through the glosso-pharyngeal nerve, for division of this nerve causes the goblets to degenerate.

All the papillæ of the tongue are made up on much the same lines, viz., an elevation of the mucous membrane, with vessels and nerves ramifying in its substance. In the coating of epithelium which the circumvallate papillæ receive are to be found the taste goblets.

In herbivora taste produces an abundant secretion from the submaxillary and lingual glands, but not from the parotid (Colin).

The papillæ in the mouth of the ox appear to serve the purpose of retaining the food in the mouth; the hard rough coating to the dorsum of the tongue is for cleaning purposes, and to retain grasp of the food in grazing. This condition is absent in the horse, who feeds with his lips and teeth.

The nerve of taste does not supply the tongue with sensation; the latter is derived from the lingual branch of the fifth pair. It is quite possible for a tongue to have lost its touch, and not its taste. The motor power is derived from the twelfth pair of nerves, or hypoglossal.

Hearing.

The arrangement of the ear is best understood if we describe it as consisting of two cavities containing air, placed side by side but separated by a partition, one of the cavities being brought into contact, by means of a flexible

bridge, with a membranous and rigid apparatus containing fluid. The cavities are the external and middle ear; the apparatus containing fluid is the internal ear; the partition between the external and middle chamber is the tympanum; and the flexible bridge connecting one air chamber with the internal ear is composed of the bones of the ear or auditory ossicles.

The vibrations of sound are collected by the external ear, which from its funnel shape is eminently calculated to concentrate them. From here they are directed on to the tympanum; this being set in vibration, the handle of the malleus, then the incus, and lastly the stapes, are also moved; and the latter being attached to a membrane in contact with fluid, the vibrations of the stapes are transferred to the fluid or perilymph, by which means a special impression is made on the nerve endings in the cochlea and so conveyed to the brain.

It is therefore in the internal ear where the proper organ of hearing is contained, and to which the eighth pair of nerves is distributed; and the arrangement is so peculiar that we must momentarily glance at it.

The internal ear consists of a cavity termed 'the labyrinth,' composed of the vestibule, cochlea, and semicircular canals. All these, with the exception of two small surfaces, are entirely covered with bone, yet within it we find a membranous labyrinth containing a fluid termed 'the endolymph,' and in the space between the membranous and osseous labyrinth is a second fluid termed 'the perilymph.' Within the coils of the cochlea are spread out on a special membrane some remarkable cells or organs, termed 'the organs of Corti'; their general arrangement resembles the keyboard of a pianoforte, and in connection with them, through the medium of the auditory epithelium in which they terminate, are fibres of the special nerve of hearing.

The eighth pair of cranial nerves supplies the special sense of hearing. The nerve is remarkably soft, and its fibres very fine. It gives off branches to the vestibule, cochlea, and semicircular canals.

The tympanic membrane is placed obliquely across the canal of the external meatus, and owing to its attachment to the malleus on the opposite side, it does not present a plane, but a concave surface towards the external ear. It is not tightly stretched across the space; by its attachment to the malleus excessive vibration is prevented, for this connection acts the part of a damping apparatus.

The bones of the ear transmit the vibrations from the tympanic membrane to the internal ear. The small bones have a certain amount of movement on each other, and there are special muscles for bringing it about; by means of these movements the tension of the membrane may be altered. As before mentioned, this chain of bones lies in the middle ear, which is also an air cavity deriving its supply through the Eustachian tube. It is necessary for the perfect production of sound that the same atmospheric pressure should exist on both sides of the tympanic membrane, and this is provided for by the Eustachian tube.

Whatever part those remarkable sacs (confined solely to solipeds) are intended for—viz., the **guttural pouches**—it is probable, from their anatomical connection, that they take some part in the sense of hearing, perhaps that of supplying the needful amount of air to the middle ear. The actual use of the guttural pouches is involved in obscurity, but we may provisionally consider them as part of the middle ear. In man, acuteness of hearing is produced by listening with an open mouth; the fact that the horse cannot breathe through the mouth may explain the presence of these large air-sacs beneath the skull; in other words, they are probably associated with acuteness of hearing.

The tension of the tympanic membrane, produced by the muscles acting on the small bones of the ear, assists in protecting the internal ear from violent noises, and the same movement which slackens or tightens the drum-head increases or decreases the pressure on the perilymph of the internal ear.

The stapes being fixed against the membranous labyrinth through a foramen in the osseous structure, every alteration

in the pressure it exercises transmits movement to the fluid of the internal ear, and excites the terminal organs of the auditory nerve which are lying free in the endolymph.

In the cochlea the nerve endings of the eighth pair are distributed over a large surface, which is one explanation of the peculiar shape of the part, and in connection with the nerve endings are the peculiar rods of Corti; these are so arranged that they are supposed to each be capable of vibrating to its own particular tone, and thus really striking its own note.

The excessively hard bone in which the internal ear is lodged, with its central fluid medium, are both of the highest acoustic value.

The semicircular canals, though they undoubtedly take some part in hearing, are particularly connected with maintaining the equilibrium of the body, and of keeping the mind acquainted with its position. This remarkable function is probably carried out by alterations in the position and pressure of the fluid contained within them, which results from every movement of the head (see p. 281). Division of these canals causes the most remarkable irregularity in the movements, and a side-to-side or upward movement of the head.

In certain parts of the vestibule are found small particles of calcareous matter termed **otoliths**. They are brought closely in connection with the nerves in the labyrinth, and produce upon them more intense impressions than would be produced by fluid alone.

Touch.

The sense of touch in the lower animals is developed to a considerable degree in those parts of the body used for contact purposes, such as the muzzle and the feet (where probably special nerve endings exist), and generally throughout the skin, especially in the horse, in which a very acute sense of touch exists, though no special touch organs have been found in connection with the nerves of the skin.

The sense of touch is for the purpose of rendering the

animal acquainted with its surroundings. In the lips, where we find the most exquisite sensibility, this sense is developed not only for the purpose of distinguishing the different varieties of food, but for ordinary touch purposes, the lips of animals corresponding to our fingers. In the horse the nerves supplying the long papillæ of the skin of the lips run to their extreme termination, the papillæ being thrown as finger-like processes into the substance of the epithelial layers, and almost reaching to the free surface.

The tactile sensibility in the foot of the horse enables him to be acquainted with the nature of the ground over which he is travelling, though that this is not absolutely essential to his safety in progression, is proved by the results of plantar neurectomy. I have suspected the presence of, but not yet found, definite touch organs in the foot.

The long feelers, or hairs, growing from the muzzle are all endowed with extreme sensibility; this is brought about through their close connection with the nerves of the skin.

We cannot explain why it is that the different impressions of touch or pain can be so accurately defined by the peculiarity of the impression conveyed. The impression of a prick, a cut, or a burn, touch, itching, etc., produce unmistakable evidence of the nature of the substance causing the impression.

Through the nerves of the mucous membrane of the mouth impressions are carried to the brain, impressions which in horses convey unmistakable evidence to the animal of the strength of will or weakness of his rider.

CHAPTER XVII.

THE LOCOMOTOR APPARATUS.

The muscles are attached to bones, which form by their movements on each other angles of varying size. These angles are opened and closed during progression, and the mechanical aid which is introduced to effect this is that of the lever.

The lever is composed of a power, fulcrum, and weight, and, according to the relative position which these occupy, we have formed a lever of the first, second, and third order.

In a **lever of the first order** the power is at one end, the weight at the other, and the fulcrum between the two. If we try to move a heavy box by placing a crowbar beneath it, and a block under the crowbar, we are employing a lever of the first order, the box being the weight, the block the fulcrum, and the hand of the operator through the crowbar the power. The muscles which extend the head act also as a lever of this order, the head being the weight, the occipito-atloid articulation the fulcrum, and the muscles of the neck the power. When the angle formed between the scapula and humerus is reduced, the triceps forms a lever of the first order, the muscle being the power, the elbow the fulcrum, and the limb below the weight. In extension of the hind-leg the gastroc muscles are the power, the hock-joint the fulcrum, and the leg below the hock the weight.

This is principally a lever of extension, and exists all over the body. It is a lever of power, for if the long-arm be

5 feet, and the short-arm 1 foot, a power of 1 lb. at the long-arm will support a weight of 5 lbs. on the short-arm; but it is to be noted that as a lever increases in power it loses in speed.

In the **second lever**, which is a rare one in the body, the weight is placed between the fulcrum and the power, as in a wheelbarrow, the wheel being the fulcrum.

When the leg is fixed on the ground the muscles of the olecranon act as a lever of the second order, the ground being the fulcrum, the triceps the power, and the body through the elbow-joint the weight. The same applies to the gastrocs when the weight is on the limb and the foot on the ground.

In the **third order of lever** the power is between the fulcrum and weight. It is the lever of speed, and what it gains in speed it loses in power. It is also the lever of flexion, and examples abound in the body; the flexor brachii is one, the weight is the leg below the elbow, the power the muscle at its insertion into the radius, and the fulcrum the elbow-joint above. This is a wasteful lever, but an essential one in the limbs. The nearer the power is to the fulcrum, the greater the flexion obtained with the least amount of muscular force, and the same remark will apply to the first lever. Other examples are the masseter muscles, flexor metatarsi, the psoas magnus, the muscles which flex the head, etc.

In nearly all cases the fulcrum of the lever is formed by a joint, which is fixed or rendered rigid by other muscles during its action. Antagonistic muscles are not relaxed during the contraction of their opponents, nor are they contracted. They may help the antagonistic muscles to return to their position of rest.

Groups of muscles act together; this co-operation admits of certain points being fixed, or increases the effect, or gives the movement a special direction (Foster).

The reason why the third lever is more frequent than the others, is due to the fact that the chief movements of the limbs are directed to moving comparatively light weights

through a great distance, or through a certain distance with great precision, rather than moving heavy weights through a short distance (Foster). In connection with this we may say that the weight of the fore-leg, cut off at the elbow, of a cavalry horse was found to be 17 lbs. 8 oz.; cut off at the knee, through the upper row of bones, it was found to weigh 7 lbs. 10 oz.; one fore-foot with corona weighed 2 lbs. 3 oz., and the hind-leg, cut off at the hock-joint, weighed 10 lbs. 9 oz.

It is very necessary to be clear on this question of levers, and not to adopt too rigid a mechanical view of them. The point of importance to which I would draw attention is, that what will form a lever of one order in a certain position of limb, forms a lever of another order in a new position. We have given examples of this in the triceps extensor brachii acting in the one instance as a lever of the first order, and then as one of the second. The nature of the lever depends upon the position of the body, so that Colin proposes the term 'alternative lever.' He also speaks of a 'composite lever,' where the power in the same position of limb acts in two distinct ways, and he gives as an example the flexor metacarpi externus acting as a lever of the first order above the knee through its insertion into the trapezium, and as a third order of lever below the knee through its insertion into the external metacarpal bone.

The same care must be taken also in viewing muscles simply as extensors or flexors. Stillman points this out very clearly, and lays stress on the fact that some muscles may act as flexors and extensors at the same time, and he very rightly impresses the importance of taking into consideration in animal locomotion some other action of muscles than that of flexion, extension, adduction, and abduction, viz., the function of *propelling*, which he believes to represent 85 per cent. of the work of the horse's muscles.

It is most important, however, to remember that propelling is not a power apart from flexion and extension, but the result of them.

The difference existing between the articulation of the

fore and hind limbs with the body, has until recent years been the cause of considerable error being promulgated. It was previously supposed that the muscular attachment of the fore-leg to the trunk indicated that the body was simply slung between the fore-legs, the latter acting as props whilst the hind-limbs did the work. Instantaneous photography has shown us that the fore-limbs not only act as props, but also as most efficient propellers of the body, especially in the gallop, where by measurement it has been shown that one fore-leg will propel the body a distance of 10 feet and raise its centre of gravity 4 inches.*

By means of the fore-legs the horse is enabled in draught to assist his hind-legs in stopping weights.

Joints are formed wherever two bones come into contact. Dealing only with those joints found in the limbs, which are of the most practical interest, we find we have ball-and-socket joints (as in the hip), hinge-like joints (as in the hock), gliding joints (as in the knee), and spiral joints (as in the stifle). All these joints are coated with articular cartilage and lubricated with synovia.

Synovia is a viscid, yellow, alkaline fluid containing proteids, mucin, and salts. The viscidity of synovia is due entirely to the mucin it contains, and it confers on synovia its slippery nature. There is no difference between the synovia of joints and that of bursæ.

It is said that the amount of synovia in a joint is greater in animals at rest than in those at work, but its bulk appears to be due to an increase in the watery material, whilst the proteids are decreased; the salts, on the other hand, especially those of sodium, exist in a larger proportion than in the synovia of working animals.

The bursæ in the limbs of the horse are very important structures. They are placed where the tendons pass through bony channels, as at the back of the knee, and also may be turned to useful advantage as pulleys, as in the sesamoids at the fetlock, or the calcis in the hock. Without them the rapid movements of the limbs would be impossible,

* 'The Horse in Motion' (Stillman).

and that the strain and wear and tear is considerable we know from practical experience.

The only joint I propose dealing with in detail is one the action of which I believe to be universally misunderstood. I refer to the perfect hinge-joint formed by the articulation of the tibia with the astragalus.

Hock Joint.—Solipeds appear to stand alone in having the ridges of the astragalus obliquely placed, instead of vertically as in ruminants. The ridges are oblique in the horse, and some considerable difference in the action of the limb is the result. It is usual to speak of the screw action of the hock produced by the oblique ridges of the astragalus. This screw action I believe to be an entire misconception; the ridges on the astragalus do act as a screw, but not on the hock. *The effect is on the stifle,* and produces that remarkable stifle action particularly well seen in trotters. If the ridges on the astragalus turned the hock outwards, every horse would travel as if he were 'cow-hocked.' I hold that the leg below the astragalus is carried directly forwards; when, however, it comes to the ground, and the body passes over it, it is not uncommon in some horses to observe a considerable twist *outwards* of the hock-joint, the toe being turned in; this is due to the *ascent* of the tibia on the astragalus *turning in the stifle,* the result of the leg being fully extended.

The cuneiform bones of the hock have a movement on each other and the astragalus, which is always in the one direction, viz., obliquely outwards.

The object of the stifle being turned outwards during the flexion of the leg is to clear the abdominal wall, and the reason why solipeds have oblique ridges on the astragalus, and ruminants vertical ones, is that the ribs of the latter class are short, and do not come near the pelvis (as in the horse), and therefore the abdominal wall is not in the way.

A spring or automatic flexion action in the hock has been described, such as may be readily observed in the dead leg, when if the hock be flexed slightly it either flies back,

or completes its revolution with a jerk. This condition does not exist during life, nor after death until rigor mortis occurs; it is produced by the lateral ligaments of the hock-joint, and is purely a post-mortem condition.

The flexor metatarsi muscle is remarkable in having a tendon running its whole length, so that from the origin at the femur to the insertion at the front of the hock is a stout tendinous cord. When the muscle acts the hock is flexed, but the use of the tendon running from origin to insertion is not at first sight quite clear. Chauveau considers that it automatically flexes the hock, but tendons are devoid of any such power; and it appears to me that its sole function is to relieve the muscle when the animal is standing or sleeps standing. Though a flexor of the hock, we must remember that when muscles which perform flexion and extension are acting together with equal force no movement results. Such is the case when the weight is on the limbs and the animal at rest. When a horse is at rest his gastroc muscles and flexor metatarsi are acting in opposite directions, and equally—the one is trying to close the femoro-tibial angle, the other is keeping it open; it is the function of the tendinous portion of the flexor metatarsi to keep this angle open without any muscular effort.

Briefly reviewing some of the other joints, we find that the **Stifle** is the largest in the body; the cause of its rotation has just been described. One chief function of this joint is that of rendering the limb firm and rigid when the foot is on the ground while the body is at rest, and this it does by the contraction of the muscles inserted into the patella; if the latter bone be kept fixed on the upper part of the trochlea of the femur, no flexing of the hock or stifle can occur. This experiment can be readily tried on a horse just destroyed; the limb having been extended, the simple pressure of the hand on the crural muscles is sufficient to prevent the bending of the hock unless considerable force be employed. No bending of the hock can occur if the foot be kept extended; the first movement in the advance

of the leg and the flexing of the hock and stifle, is that the foot is flexed. In a certain surgical condition, commonly known as dislocation of the patella, the limb is rigid from the stifle to the hock; but, though the foot may be flexed, neither hock nor stifle responds, owing to the patella being fixed. I believe, in the majority of these cases, that the patella is not fixed from dislocation but from spasm of the patella muscles.

The amount of movement in the stifle is so considerable, that to admit of it being carried out with perfect freedom the convex condyles of the femur play in cups formed of cartilage on the upper surface of the tibia. It will be noticed that the patella does not play up and down on the femur, as at first sight we might expect, but rather that the femur plays on the patella by the opening and closing of the femoro-tibial angle.

The **Hip** is a cup and ball joint; the range of movement obtained by it in the horse is limited by the insertion of the ligamentum teres and pubio-femoral ligament into the inner side of the head of the femur, and not into its centre as in most other animals. This is said to be the reason why the horse rarely 'cow-kicks.' The lengthening of these ligaments, according to my unpublished observations, accounts for 'cow-hocks' in horses.

The **Shoulder-joint** is remarkable for the considerable surface afforded by the humerus and the small surface of the scapula, the object being to obtain a large range of motion.

The **Elbow** presents an articulation with ridges which influence the turning outwards of the knee in progression; if the knees are turned out too much the leg below is thrown in as it is brought forward, and in this way 'brushing' and 'speedy cutting' is produced; but in the knee-joint a provision exists to counteract this movement.

The **Knee** consists of three main joints and numerous minor ones; the upper joint possesses the largest range of motion, whilst the lower joint practically does not open. Probably such defects as speedy cutting and its opposite

condition, 'dishing,' are influenced not only by the elbow, but by the shape of the articular surfaces between the radius and upper row of bones.

The radius is peculiar in presenting on that articular surface next the knee a concave surface anteriorly and a convex one posteriorly; these form two condyles, of which the inner is more curved than the outer. The outer condyle plays on the trapezium, cuneiform, and lunar: the inner condyle plays solely on the scaphoid. When the knee is flexed the influence of the condyles is seen; the concave articular surface of the radius is removed from the surface of the bones of the knee, and the convex articular surface appears as the joint grows wider. The inner condyle being larger than the outer depresses the scaphoid, so that a very important movement occurs between the scaphoid and lunar; this action of the radius on the scaphoid throws the foot slightly outwards, probably with the object of enabling it to clear the opposite limb. I believe that an examination of the knees of 'dishing' horses will show that extreme curvature of the inner condyle of the radius is the cause of the action, in the same way that turned-in elbows and alterations in the curvatures of the radius and humerus will probably account for horses throwing the lower part of the leg inwards, and thus 'brushing' or 'speedy cutting.'

The **Fetlock** forms a flexible articulation; in a state of repose the greater part of the horse's weight is borne on the posterior half of the metacarpal articulation, and the articular surface of the sesamoids. The influence exercised by the sesamoids by being attached both above and below to ligamentous structure is dealt with in the next paragraph. For the movements of the foot-joint, see the Chapter on the Foot.

The **Function of the Suspensory Ligament** has been a fruitful source of discussion. Its chief use, no doubt, is to support the fetlock; in no other way could a joint placed in such a part of the limb, possessed of so much motion, and exposed to such concussion, be supported. Though

ligaments and tendons are held to be non-elastic, yet we must claim for the suspensory ligament a little more elasticity than would be obtained if the sesamoids were united by bony tissue to the metacarpal; and the pleasantness and freedom from jar experienced in the riding-horse is due to the suspensory ligaments. But Stillman claims for it a function which he believes to be demonstrated by instantaneous photography, viz., that it acts the part of a spring, flexing the fetlock sharply when the weight is taken off it, and explaining why the dirt is thrown out of the feet of a galloping horse. The sharp picking up of the foot from the ground in walking (a movement so rapid as almost to defy detection) is probably assisted by the suspensory ligament. Besides these functions, the suspensory ligaments assist the horse to stand whilst sleeping.

Function of the Check Ligaments.—Horses are enabled to sleep standing, and remain for some considerable time without lying down, by means of a singular arrangement of check ligaments which exists in both fore and hind limbs. The flexor tendons support the weight, the extensors keep the limbs rigid. In order that the strain of supporting the weight may not be placed on the muscles of the arm, both flexor tendons, one above and both below the knee, receive a large branch of ligament from the radius and metacarpus respectively. These are attached below the muscular portion, and so cut off the latter entirely from the strain of standing in one position for any length of time. This is also assisted by the suspensory ligament running from the metacarpus to the back of the fetlock. If the suspensory ligament be divided, the fetlock does not come to the ground; if the perforans be divided, a slight sinking of the fetlock is the only change. To bring the fetlock to the ground, both flexors and suspensory ligament must be divided, which demonstrates that all three support the weight while standing, and by their peculiarity in attachment enable the animal to sleep in the upright position.

Further, the horse is enabled to stand whilst sleeping by

means of the fascia of the arm and thigh; both of these are attached to the muscles and tendons of the part, affording them considerable support of a non-muscular nature; particularly is this the case with the fascia of the thigh.

Centre of Gravity.—Whether the horse be at rest or in motion, the position of his centre of gravity is an important one for our consideration. The centre of gravity at rest is fixed, but during motion it oscillates from side to side, depending on the position of the body and the pace.

At rest the centre of gravity must always fall within the base formed by the four feet, or the body is no longer in stable equilibrium. Owing to the fact that more weight is carried on the fore than on the hind legs, the centre of gravity lies nearer to the elbow than the stifle. If a vertical line be dropped just behind the ensiform cartilage of the sternum, and intersected by a horizontal one passing through the lower part of the middle third of the body, the point of intersection is the centre of gravity; this is the rule given by Colin. We may say, speaking roughly, that the vertical line passes about six inches behind the elbow, the horizontal just below the shoulder-joint; the centre of gravity is where these intersect. It is obvious that the position of the centre of gravity will vary with different horses, but not to such an extent as to seriously affect the truth of the above statement.

Distribution of the Weight of the Body.—The fore-legs carry more weight than the hind, which is perhaps, the reverse of what might be expected; but if a horse be carefully weighed, it is found that the fore-legs take more than one-half the body weight. The position of the head considerably affects the weight on the legs. Thus, if the head be raised up when the fore-legs are weighed, the latter will be found to be carrying over 20 lbs. less weight than if the head were dependent. The practical application of this fact is obvious—keep a stumbler well in hand. A horse's head weighs between 40 and 50 lbs.

When a man is on the horse's back, it is found that 66 per cent. of his weight is carried on the fore-legs, and 34 per cent. on the hind; the amount of weight on the fore-legs is increased by leaning forward in the saddle, and decreased by leaning back.

An explanation why fore-legs are worn out earlier than hind is afforded us by what we now know of the physiology of locomotion, viz., the fore-legs act as propellers of the body, and owing to their being close to the centre of gravity, they bear the largest share of the weight of the body and the weight of the rider.

In the **act of standing** the body is supported on four props; two of them have only a muscular attachment to the trunk, the other pair are united by a ball and socket joint. It is unnecessary to allude by name to the muscles connecting the fore-leg with the trunk, excepting to mention the serratus magnus, through the medium of which the body is principally slung on the scapula.

No matter what the position of standing may be, or the condition under which the horse is standing, he never in a state of health keeps his fore-feet in any other position than together; one fore-limb advanced in front of the other is abnormal. On the other hand, it is very rarely that one ever sees a horse standing square on both hind-legs, he is invariably resting the limbs alternately. Some years ago I drew attention* to this as being an explanation of the exemption of the hind-limbs from navicular disease. By this process of resting, the compression of the navicular bone between the body and the perforans is relieved. The horse only learns to do it in the fore-legs when too late.

When the horse is feeding off the ground, he always has to advance one fore-leg a considerable distance in front of the body, owing to the shortness of his neck.

In the act of standing the rigidity of the bony column of the leg is maintained by the extensor tendons, each phalanx having an extensor attached to it, viz., the extensor metacarpi leading to the large metacarpal bone, extensor pedis

* *Veterinary Journal*, 1886.

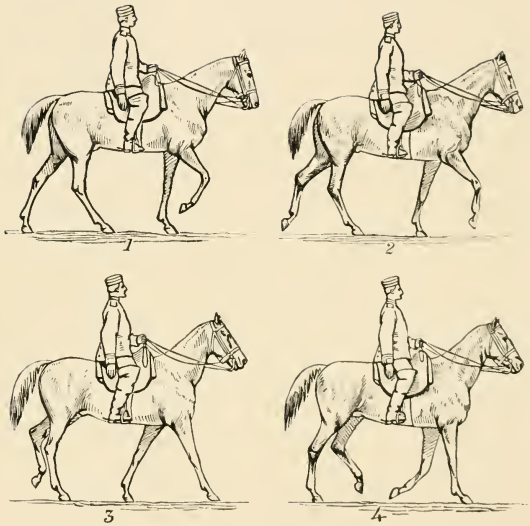

FIG. 37.—THE WALK.

From instantaneous photographs by Ottomar Anschütz. (Ellenberger's 'Physiologie.')

to the corona and pedis, receiving also a slip from the suspensory ligament, and extensor suffraginis to the suffraginis. This latter receives a strong slip of ligament from the outside of the carpus, which entirely takes off the strain from the muscle, and keeps the tendon taut during sleep. The action of the tendons and ligaments of the hind-leg in the act of standing has been described on p. 325.

When a horse falls at a walk or trot, he injures his knees; but when he falls (which is sometimes the case) through sleeping standing, he invariably damages his fetlocks.

Locomotion.—We have next to study the question of locomotion in the horse, and describe how the legs are moved during the different paces. It will be remembered that our knowledge of this subject chiefly depends upon instantaneous photography, the pioneers in the field being Stillman and Muybridge.*

The axiom laid down by Stillman is that 'perfect quadrupedal locomotion requires *uniform support to the centre of gravity, and continuous propulsion by each extremity in turn.*'

The **Walk** is the slowest pace, and is executed in a perfectly definite manner. In the first stage the body is balanced on three legs, in the second stage on two diagonal legs, in the third stage on three legs, and in the fourth on two lateral legs, and the next movement brings us back to the first stage, only with different legs employed (Fig. 37).

We will now trace the movements in each stage: The horse advances one fore-leg—say, the off (1)—and he is left standing on the near fore, near hind, and off hind—this is the first stage; in the second stage the near hind is picked up, and the animal is standing on the near fore and off hind, viz., on diagonal legs (2); in the third stage the off fore has come to the ground, and the animal is balanced on both fore and the off hind legs (3); in the fourth stage the near hind is advanced to be placed over, or in advance of, the track of the near fore; to make room for it the near fore is advanced, and the horse is left stand-

* 'The Horse in Motion.'

ing on two lateral legs, viz., off fore and off hind (4); the next movement brings the horse into the first position, the hind-leg coming to the ground first leaves him on the off fore and both hind-legs, and the near fore is being advanced to be followed by the off hind—it is simply the first stage with the near fore leading instead of the off fore.

The fore-leg remains on the ground for a longer period than it takes passing through the air; this can be seen perfectly in watching the animal, and comprises the period during which the body is passing over the limbs. The movement in the air both of fore and hind legs is so extremely rapid as almost to defy detection, so far as defining the changes in the direction and shape of the limb.* The snatching up of the foot from the ground is the quickest movement. Stillman refers the snatching up to the spring or rebound of the suspensory ligament.

In walking, the majority of horses rarely extend the knee any great distance beyond a vertical line dropped from the shoulder. A sudden movement of the extensors now straightens the leg, and the foot is placed down flat or heel first. If the leg is not fully straightened by the extensor muscles, the foot comes to the ground toe first, with the knee slightly bent, and a stumble follows.

It appears to be a matter of indifference which fore-leg an animal starts the walk with.

Figs. 38 and 39 show the curves or paths described by both fore and hind limbs in the walk, after Marey and Pages. Examining these curves *from the time the foot leaves the ground until it touches it again* (Fig. 38, B), we find that the shoulder-curve runs slightly upwards, due to the limb being advanced; the elbow-curve runs rather downwards, due to the limb being extended; the knee shows a marked upward curve, and then a fall as extension occurs; the fetlock also shows a well-marked curve, due to its flexion and then extension. The curve shown by the

* Stillman states that if the speed of the horse be 25 miles an hour, the foot which is in the air and travelling forward is moving at the rate of 50 miles an hour.

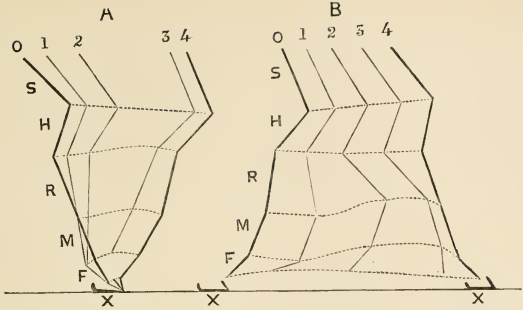

Fig. 38.—Path Described by the Joints of the Fore-limb at the Walk: A, while the Foot is on the Ground; B, during the Time it is in the Air.

S, scapula; H, humerus; R, radius; M, metacarpus; F, fetlock; A—0 is the position in which the leg makes contact with the ground; 4, the position at which it leaves it; B—0 is the position in which the limb leaves the ground, and 4 at which it meets it; X is the foot; 1, 2, and 3, various phases during progression. Observe the sinking of the fetlock at A, 1 and 2, as the weight comes on the limb. (Marey and Pages.)*

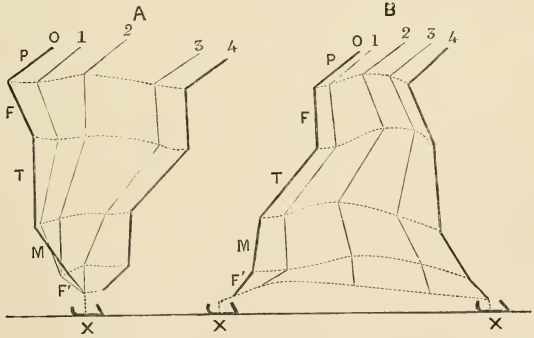

Fig. 39.—Path Described by the Joints of the Hind-leg during the Walk.

P, pelvis; F, femur; T, tibia; M, metatarsus; F', fetlock; X, foot. In other respects the description of Fig. 38 applies. (Marey and Pages.)

* Goubaux and Barrier, 'L'Extérieur du Cheval.'

foot is a large and gradually increasing one; it then rapidly descends as extension occurs.

Marey and Pages' foot-curve, which is the only one I have worked out, agrees with my results, which were obtained by walking the horse past a vertical piece of prepared canvas, and a blacklead pencil being attached laterally to the foot the path was readily traced on the canvas.

The curves described *by the fore-limb from the time it touches the ground until it leaves it* are shown in Fig. 38, A. The shoulder sinks, the joint coming nearer the ground due to the forward movement of the body, which, from my observation, is the cause of collar-galling when collars are too wide, for the depression of one shoulder and the elevation of the opposite one produces considerable side-to-side movement, and consequently great friction. While the body is passing over the leg the elbow slightly rises, due to the ascent of the fetlock; this also produces a well-marked curve in the path of the knee, the fetlock-curve is naturally the steepest; we notice that there is first a sinking backwards in the fetlock curve before it rises; this occurs at the moment the weight of the body commences to pass over the foot (Fig. 38, A, 1 and 2).

Following now the curves of the hind-limb *from the time it leaves the ground until it meets it again* (Fig. 39, B), we find the stifle-curve rises and then slightly falls as the leg touches the ground; the hock-curve is highest at the first half of the movement, and then falls; the fetlock-curve rises, being greatest at the middle of the movement, and then falling; the foot-curve is greatest at the commencement of the movement.

In examining the curves of the same limb *from the time it reaches until it leaves the ground* (Fig. 39, A), there is a well-marked up-and-down curve in both hip and stifle, that of the stifle being particularly marked towards the end of the movement, and due to the extension of the leg; the hock-curve rises the whole way, whilst the fetlock-curve is rather a flat one compared with the fore-leg.

The **Trot** is a very simple pace to analyse (Fig. 40), for the body is supported on diagonal legs (1), which by their propulsion drives it off the ground, so that there is a period during which there are no legs on the ground (2). When the body comes to the ground again the next pair of diagonal legs receive it (3), and once more propel it oft the ground. There are thus three stages to the trot; the body in two of them is supported by diagonal legs, and in one of them the body is in the air.

The trot appears to be the only pace in which instantaneous photography has supported the conventional notions of this movement. We can see the trot, first, because it is a simple pace, and secondly, because the body is comparatively so long in the air. When a horse falls at the trot, he does so through not bending his knee sufficiently in bringing the leg forward, and the toe touches the ground, or if the extension of the knee is not perfect he also falls. When the knee has been well bent and the leg brought forward, the limb is then sharply extended and the foot placed down flat or heel first.

Marey and Pages' curves of the fore and hind limb during the trot are seen in Figs. 41 and 42. Observe the knee-curve as the limb is in the air. The hock-curve in Fig. 42 is much flatter than one would have expected, whilst the foot-curve is a big one.

In the **Amble** the horse, instead of using diagonal legs uses the lateral limbs, so that off fore and off hind are on the ground instead of off fore and near hind. A horse may amble both at the walk and trot, in this respect resembling a camel. There is no doubt that it is perfectly natural for some horses to amble; many others are taught the pace, as it is a particularly pleasant one for the rider.

In the **Canter** (Fig. 43) the body is pushed upward off the ground by one fore-leg—we will say the off fore (1)—the near fore leading, and both hind being off the ground; in the next stage all the legs are off the ground though the feet are no great distance from it (2); in the third stage the body returns to the ground, alighting on the near hind-leg,

Fig. 40.—The Trot.

From instantaneous photographs by O Anschütz. (*Ellenberger.*)

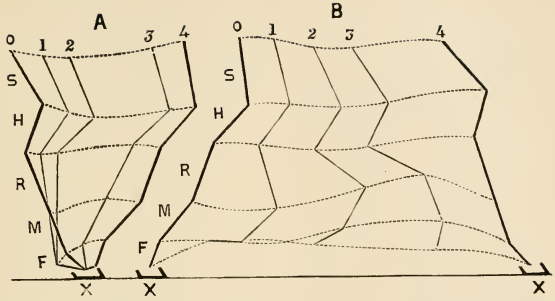

FIG. 41.—CURVES DESCRIBED BY THE FORE-LEG DURING THE TROT.

The description of Fig. 38 applies. (Marey and Pages.)

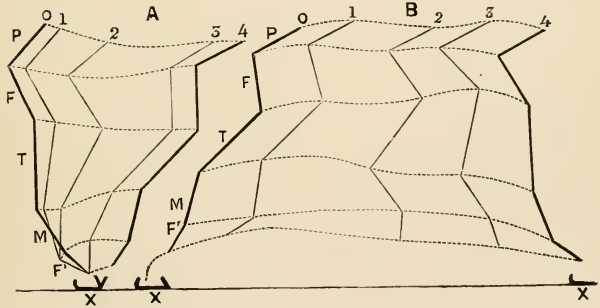

FIG. 42.—CURVES DESCRIBED BY THE HIND-LEG DURING THE TROT.

The description of Fig. 39 applies. (Marey and Pages.)

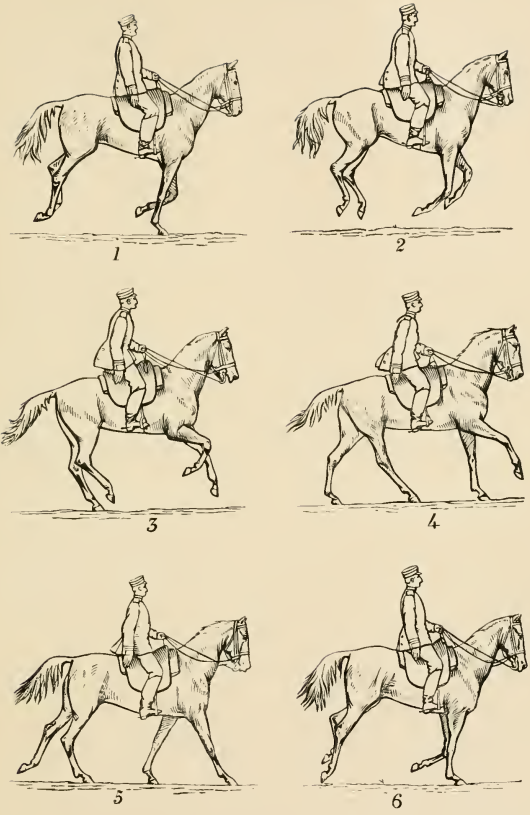

Fig. 43.—The Canter.

From instantaneous photographs by O. Anschütz. (*Ellenberger.*)

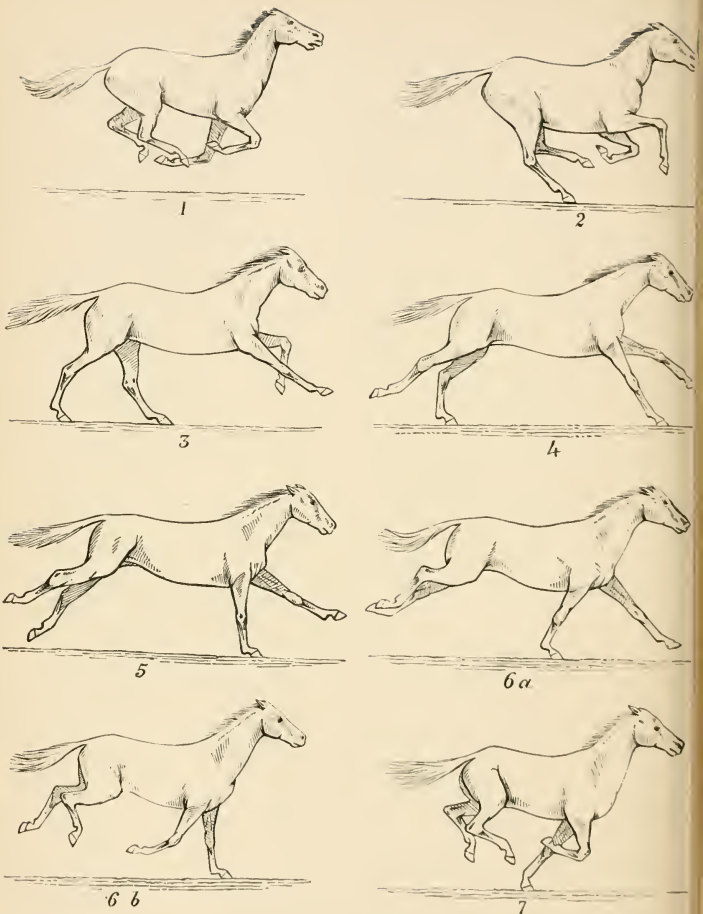

Fig. 44.—The Gallop.

After Stanford, Muybridge, and Stillman. (*'The Horse in Motion.'*)

which is not placed under the centre of gravity, as in the gallop, but behind it, the animal being balanced on one limb only (3); in the fourth stage the off hind and near fore come to the ground together, so that the body is now balanced on three legs, viz., near fore and both hind (4); in the fifth stage the off fore comes to the ground, but as it does so the near hind rises—the animal is still left on three legs, viz., both fore and off hind (5); in the sixth stage the near fore and near hind, and, slightly later, off hind, leave the ground, the horse being balanced on the off fore only (6); the next movement is a repetition of the first, the off fore pressing the body upwards.

The **Gallop** is a very difficult pace to describe, and the analysis I give of it here is from one of Mr. Muybridge's numerous and beautiful instantaneous photographs (Fig. 44). To this gentleman the scientific world is indebted for an accurate knowledge of how animals use their legs in progression.

The **Gallop** consists of seven stages. We will elect to describe it from the time the animal is in the air, no legs being on the ground, but all four of them brought well under the body; this is the first stage (1). In the second, one hind-leg, say the off, comes to the ground (2); in the third stage the near hind comes to the ground, the horse now being balanced on two hind-legs, both fore being in the air (3); in the fourth stage the off fore comes to the ground, but the horse is not balanced on three legs as in the canter, for at the moment the off fore came to the ground the off hind was extended, leaving the animal on diagonal legs, viz., off fore and near hind (4); in the fifth stage the near hind leaves the ground, the animal being balanced on one fore leg, in this case the off fore (5); in the sixth stage the near fore comes to the ground (6*a*), and the off fore leaves it (6*b*)—the body is, therefore, again supported on one fore leg; in the seventh stage the body passes over the near fore leg (7), and by a contraction of its muscles the entire weight is lifted off the ground, and the body propelled forwards and upwards (1).

The points of importance to observe in the gallop are: that the heel of the foot comes to the ground first, that the hind-legs break the shock of the falling body, and that the fore-legs share in propelling the body as much as the hind. The latter is a truth which was never anticipated until Mr. Muybridge published the results of his labours.

In examining the track of a galloping horse it is remarkable to observe what a very straight line the hoof-marks leave, showing that each foot is brought well under the centre of the body.

When a horse gallops, no matter how fast the pace, the fore-feet never extend beyond a vertical dropped from the muzzle.

In the **Jump** (Fig. 45) the horse rises to it by the propulsion upwards which the fore-legs give to the body (1); both hind-legs now being fixed on the ground, he gives the propulsion through these to his body, the hocks at the same time being greatly flexed to enable the feet to clear the obstacle (2). In alighting on the other side he does so through the medium of both fore-legs, one following the other (3); instantaneous photography appears to disprove the theory that in the jump a horse alights on the hind-legs.

In **Rearing** the hind-legs are brought well under the body, the head and neck thrown up, and the propelling power of the fore-legs directs the body upwards, where it is sustained by the muscles of the back and loins. So long as the centre of gravity falls within the base formed by the hind-feet, the body is in a position of stable equilibrium; but if it passes outside this base, the horse comes down on to the point of both hocks, and may either roll over on his side or go directly backwards. If the latter, the first part of the body to strike the ground is the occiput. In this way I have met with many fractures of the base of the skull through *contre coup*, and also a fracture of the dentata from direct violence.

In **Kicking** with both hind-legs the head is depressed, and a powerful action of the muscles of the quarter and

Fig. 45.—The Jump.

From instantaneous photographs by O. Anschütz. (*Ellenberger.*)

back throws the hind-part upwards, and at the same time both legs are violently extended. A horse appears to have little or no power of kicking if his head be kept up, or his tail be fixed down.

In **Buck-jumping** the animal springs bodily off the ground, the back is violently arched, and the head depressed between the fore-legs.

In **Lying down** the horse brings his four legs together under his body, bends both knees and hocks, the knees and chest touching the ground before the hind-quarters. Whilst down he either lies extended on his side, or seated on his chest, two lateral legs being under the body, and two outside it; if on his near side, the near fore-foot is close to the breast-bone, the elbow resting on the ground, the hind-foot under the abdomen, the off fore-foot lying close to the off elbow, but outside it as a rule, and the point of the off hock is touching the ground. A horse does not lie long in one position, owing probably to the enormous weight of his body.

In **Rising** he can only get up by extending both fore-feet in front of him. The hind-quarters are now pressed upwards, assisted by the muscles of the back, and the animal is immediately on his feet, the fore-part always rising before the hind.

The cow rises quite differently—in fact, the reverse of the horse, the hind-quarters being the first to ascend. The camel rises in the same manner.

The Normal Daily Work of Horses, the rate at which they are capable of performing it, and the power they exercise in doing so must now be briefly considered.

Rankine has laid down that the **mechanical daily work** is the product of three quantities: (1) the effort; (2) the rate; (3) the number of units of time per day during which the work is continued. Our only difficulty here is obtaining the value of the effort, which it is clear must depend upon the nature of the work, the character of the ground, the weight carried or drawn, and the physical fitness of the animal. I have dealt with this question

elsewhere,* as fully as is possible in our present state of knowledge. The whole subject requires to be gone into carefully, both mathematically and by direct experiment. In the work alluded to will be found formulæ for calculating the foot-tons of work performed both in saddle and draught, though the results can only be regarded as approximately true.

The normal work of horses would appear to be 3,000 foot-tons per diem; a hard day's work is equivalent to 4,000 foot-tons, and a severe day's work is 5,000 foot-tons. Redtenbacher places the daily work of a horse for 8 hours at 6,700 foot-tons, and Rankine's tables show† that a draught horse exercising a force of traction of 120 lbs. for 8 hours a day, performs 6,200 foot-tons of work. I think both these estimates are without doubt too high. The co-efficients of resistance I have employed in my calculations, were those determined for man by the Rev. Professor Haughton. I know of none especially calculated for the quadruped. Assuming the weight of the animal, plus the weight carried or drawn, to be equal to 1,000 lbs., then 3,000 foot-tons of work will be obtained by the following:

Walking	at	3	miles per hour	for	8·7	hours.
„	„	4	„	„	5·3	„
„	„	5	„	„	3·7	„
Trotting	„	8	„	„	1·5	„
Cantering	„	11	„	„	1	„

This table is only given as a means of conveying to the mind the value of 3,000 foot-tons of work.

The **Velocity** of the gallop has been variously stated, but it is certain that no horse has galloped 1 mile in 1 minute as is reported of Flying Childers. Firetail's mile in 1 minute 40 seconds in 1772, was beaten in 1890 in the United States by Salvator's mile in 1 minute 35½ seconds. This horse was galloped on a straight course against time, the weight carried being 7 stone 12 lbs., the age of the animal four years. The best time in a race has been quoted at

* 'Veterinary Hygiene.'

† 'Encyclopædia Britannica,' art. 'Animal Mechanics.'

1 minute 39¼ seconds for 1 mile. The most severe galloping ever recorded was at Carlisle in 1761, where, owing to six heats being run, the winner galloped 24 miles. Quibbler, in 1786, galloped 23 miles round the flat at Newmarket in 57 minutes 10 seconds.

The fastest pace at which trotting has been performed is 1 mile in 2 minutes 8¼ seconds. The horse was Sunol, the match taking place in the United States in October, 1891. The celebrated American trotting-horse Tom Thumb trotted 100 miles in 10 hours 7 minutes, including a stoppage of 37 minutes, an English mare did the same distance in 10 hours 14 minutes, including a stoppage of 13 minutes. Sir E. Astley's Phenomenon trotted 17 miles in 53 minutes.

The walking performances are not numerous. Twenty-two miles in 3 hours 52 minutes was done by Sloven in 1793.

All the old performances here quoted are from Youatt's work on 'The Horse.'

Turning now to what may be expected of ordinary horses, we find that the average walk of a cavalry horse is 3·75 miles per hour; the average trot is 7·5 miles per hour, or a mile in 8 minutes; and a fast trot is 8½ miles per hour. A cavalry gallop is at the rate of 12 miles per hour.*

The stride of horses at various paces was measured in a very ingenious manner by Stillman and Muybridge.† They give the stride at the walk as 5 feet 6 inches; at the trot between 7 feet and 8 feet; at the canter about 10½ feet; and the gallop varying between 16 feet and 20½ feet, and they even speak of a stride of 25 feet.

The question of the **Weight** which a horse can carry is one affecting the vital interests of the cavalry service; there is a great difference between the weight a horse can carry and the **effective** weight he can carry. It has been stated by Desaguliers‡ that a horse at Stourbridge carried 1,232 lbs. of iron for a distance of 8 miles! This either exceeded or must have equalled his own body-weight, and the case is probably without parallel.

* 'The Soldier's Pocket-Book,' Viscount Wolseley.

† *Op. cit.* ‡ 'Expt. Philos.,' vol. i.

The entire question of the weight a horse can carry must depend upon the pace at which he has got to carry it, but under any circumstances is largely influenced by the weight of the animal's own body. We are not far from the truth in saying that the mean weight of a riding horse is 1,000 lbs., and the question is what proportion should the weight he carries bear to his own body-weight. On this point I have made some careful observations, through its important bearing on the cavalry service, and have shown that cavalry horses should not be asked to carry more than one-fifth of their body-weight, and this conclusion will doubtless apply to all saddle horses. The one-fifth of the body-weight of a cavalry horse is roughly 14½ stones. Instead of carrying this, they carry at least 20 stone. I found in a cavalry regiment that the effective carrying capacity of the horses was between the one-fifth and one-sixth of their body-weight, and that if the horse's weight be divided by 5·67 we got a figure which represented the weight it should carry. These results were arrived at by weighing a large number of horses, the weight each being 'up to' having been previously estimated by an expert.

The physiological features of **Draught** can only be glanced at. The subject of draught is a very big one, and our information is still very incomplete.

Quadrupeds appear to be designed for the purpose of draught. A horizontal spine is not intended for carrying weight. This can only be satisfactorily met by an upright column, as in man, who, from his conformation, is essentially devised for carrying a burden; the horse, on the other hand, is constructed for hauling or draught. Youatt, in his article on 'Draught,'* points out that the reason why a horse is more suited for draught than for carrying weight, is that he can throw his weight considerably in front of his centre of gravity, the feet forming the fulcrum, and 'allowing the weight of the body in its tendency to descend to act against the resistance applied horizontally, and drag it

* 'Book of the Horse.'

forward. As the resistance yields, the feet are carried forward, and the action continued.'

Such is the theory of draught. The nature of the vehicle, the condition of the roads, the angle the trace forms with the horizontal, the presence or absence of springs, four wheels or two, high or low front wheels, and the width of the track, so complicate the question as to take it at once into the domain of pure mechanics, into which we cannot follow it.

In the light or mail stage-coach, where 10 and 11 miles an hour were attained, the strain or force of traction employed by each horse was only 40 lbs.; in the heavy coach it was 62½ lbs. for each horse.

For slow draught work at 2½ to 3 miles per hour, and for 8 hours a day (which appears to be the most suitable pace and duration of labour), a force of traction of from 100 lbs. to 125 lbs., or 150 lbs., is quoted by Youatt as being the most suitable. I have previously stated (p. 351) that I consider it probable that a force of traction of 120 lbs. for 8 hours a day is too much to expect from a horse. The higher the velocity the less the force of traction which can be employed, and the shorter the duration of labour.

It has been stated (Landois) that a horse can only drag three times his own weight, and taking as a matter of convenience his weight at 1,000 lbs., it is probable that 3,000 lbs. is the limit of his strength if tested against a dynamometer. Yet this amount is far above what it is usual to regard as the power of a horse. I have been credibly informed that a big railway horse could only exercise 1,840 lbs. when tested against the dynamometer. The limit of a horse's power is therefore a very doubtful point.

Watt found that a horse could raise a weight of 150 lbs. passed over a pulley, 220 feet per minute; this, as applied to engines, is termed 'horse power,' and is equal to 33,000 lbs. lifted 1 foot high per minute, viz., 33,000 foot-pounds per minute. This standard of comparison cannot be applied to animal labour, as it is much too high. A horse could only perform this amount for 3½ hours per diem, whereas his most useful work is performed in 8 hours.

CHAPTER XVIII.

THE FOOT.

Veterinary literature has been remarkably barren on every other subject than the foot and shoeing. It was natural, perhaps, that this subject should excite considerable interest, considering its vast importance.

The first thing which strikes one in the foot is its remarkably small size in proportion to the size of the body. Comparing the horse's foot, so far as size is concerned, with our own, the advantage in the majority of cases lies on the side of the biped. The most interesting fact which physiology has to demonstrate is that, though the foot presents a small circumference, in reality it encloses a vast area, due to the anatomical arrangement of the parts.

The amount of moisture contained in the horn of the foot is something considerable, and the rate at which it evaporates is quite extraordinary. If portions of the frog be enclosed in a bottle, in a short time the interior will become bedewed with moisture. The use of this moisture is to keep the foot elastic and prevent it from becoming brittle, and the agencies which are at work to assist this are a coating over the wall of a thin varnish-like layer of horn, which can only be seen in the unmutilated foot, and in the case of the sole by the layers of exfoliated material which accumulate as the result of the shedding of the superficial layers.

We are bound to recognise that horn containing but little moisture is in an abnormal condition; it is rigid and brittle, nails driven into the part cause it to crack, and that

elasticity on which so largely depends the natural shape and usefulness of the foot becomes impaired, or even destroyed. A museum specimen of a foot will very clearly illustrate our meaning. In its dried condition it is so brittle that, if dropped, it will occasionally fracture like a piece of glass; place the foot in water for a few days, and it comes out as fresh and elastic as though it had just been removed instead of being probably 20 years old. All the horn has done is to imbibe water, which has entered the minute canals by capillary attraction, and the brittle substance now becomes yielding and elastic.

We can see how necessary elasticity is in the foot, when we consider the concussion to which it is exposed during work, and which would inevitably lead to its destruction by fracture or otherwise unless this provision were present. Clinically we are perfectly acquainted with the fractures which do occur in the wall of the hoof from violence.

One of our main objects in shoeing should be to protect the wall from unnecessary interference; the removal of the varnish layer of the wall, and the cutting across of some thousands of horn-fibres by the unnecessary use of the rasp, lead to considerable destruction. Even, however, in the most brittle foot that portion of horn nearest to the vascular structures still maintains its elasticity.

Here is an analysis of the horn of the foot:

	Wall.	*Sole.*	*Frog.*
Water - -	24·735	37·065	42·54
Organic matter -	74·740	62·600	57·27
Salts - -	·525	·335	·19
	100·000	100·000	100·00

The frog contains the largest amount of moisture, and the wall the least.

The salts are small, and consist of sodium, magnesium, iron, and silica.

The foot may be regarded as a duplicate structure, one being a complete counterpart of, and fitting into the other.

The internal one we speak of as 'the sensitive foot,' the external cover as 'the horny foot.'

The physiological interest in the sensitive foot lies in the arrangement of its bloodvessels, the provision which exists for saving the parts from destruction by concussion, the means by which the weight of the body is supported, and the remarkable manner in which the area of the foot is increased without adding to its surface.

Vascular Mechanism.—Taking the bloodvessel arrangement, we recognise that the enormous amount of blood sent to the foot is for the purpose of growing the needful quantity of horn. There is hardly any other part of the body so vascular; even the bone of the foot is a rarified structure, like so much pumice-stone, to afford passage and protection to the vessels.

Lying as the foot does furthest from the heart, added to which is its position at the lowermost part of the body, we are led to inquire why it is that the blood is able to circulate through it so thoroughly, and if other means are at hand for assisting the force of the heart in facilitating the circulation: such means, we know, do exist. The arterial blood pressure in the foot is high, for we have gravity assisting the action of the heart and powerful elastic walls to the vessels. But though the contraction of the left ventricle is sufficient to bring the blood back to the right side of the heart from any part of the body (as we have pointed out in dealing with the circulation), it is doubtful whether this would be wholly sufficient to empty the foot of blood and keep the considerable plexus of veins full.

The venous circulation is assisted by two movements in the foot, viz., the expansion and contraction of its posterior half, and the descent and elevation of the inner foot under the pressure of the body.

There is no point in the physiology of the foot which has given rise to greater controversy than its elasticity; but we submit that it is not only anatomically provided for, but amply proved within recent years. Its provision exists in

the elastic nature of the horn, the existence of large elastic cartilages at the posterior and lateral part of the foot, and the fact that though the internal foot is a solid mass anteriorly, yet it is soft and yielding posteriorly.

The amount of movement occurring in the foot under the influence of the body-weight increases no doubt with the velocity at which a horse may be travelling; it is very small at the walk, and still less when he is made to throw all his weight on to one foot by lifting up its fellow. But even with this simple test special and delicate instruments are capable of registering the movement, and, moreover, of measuring it. I cannot here enter into a description of the apparatus employed; that used by Lungwitz is fully described,* also that employed by myself.†

There is no difficulty in seeing the movement imparted to a column of fluid circulating in these parts; for if we divide a plantar vein, and make the horse walk, every time the foot comes to the ground expansion occurs, and the jet of blood is considerably increased, and when the foot is taken off the ground the jet of blood becomes reduced.

We must accept it, therefore, as a proved fact that the venous circulation is largely facilitated by the expansion and contraction of the posterior part of the foot—during expansion the blood being driven upwards, and during contraction the veins relaxing aspirate the blood into their interior.

So perfect are these changes that there are no valves in the veins of the foot, and none are found until near the middle of the pastern. To assist the circulation, the large venous trunks at the postero-lateral part of the foot are in close connection with the lateral cartilages, and some pass through its substance.

Sensitive Laminæ.—We have now to consider the means by which the weight of the body is supported within the foot. It is universally recognised that this is carried out by the union of the horny with the sensitive laminæ. That

* *The Journal of Comparative Pathology and Therapeutics*, vol. iv. 3.

† *The Veterinary Record*, January, 1892.

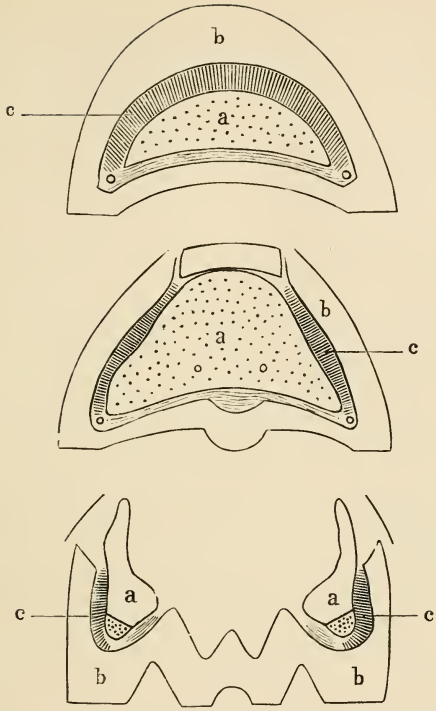

FIG. 46.—DIAGRAMS TO ILLUSTRATE THE DIRECTION TAKEN BY THE LAMINÆ AT DIFFERENT PARTS OF THE FOOT, AS SEEN IN VERTICAL SECTION.

In the top figure the section is made through the toe of the foot: *a*, being part of the pedal bone; *b*, the horny wall; *c*, the laminæ, which are practically straight, the weight being imposed from top to bottom in their length. The middle figure is a vertical section just behind the point of the frog: the laminæ, *c*, give the appearance of being placed above one another; they are rather more obliquely placed than is shown in the drawing. The lower figure is a vertical section through the posterior part of the foot: *a*, being the lateral cartilage, and *c*, the laminæ, which should slope rather more than is shown in the figure: it will be observed that the laminæ, as in the previous figure, are placed one above the other—this arrangement gives strength.

the enormous weight of the horse's body should be carried upon—or, rather, slung upon—these delicate strips of sensitive material on the one hand, and correspondingly delicate strips of horn on the other, is perhaps the most remarkable feature in the physiology of the foot. We know how firm the union is, we know the extreme difficulty of separating these two parts even by mechanical means in a state of health, and we readily recognise the delicate structure of the parts yielding this firm yet flexible union.

The horse's weight is supported in the foot by the dovetailing of 500 or more sensitive laminæ with 500 or more horny laminæ, the union being made the more complete by each primary sensitive and horny lamina containing 100 or more secondary laminæ. These laminæ afford an immense surface of support, which is longest at the toe, shorter at the quarter, and still shorter at the heel; but though the slinging surface is so much shorter at the quarters and heels, yet its strength is increased by the direction in which the weight of the body comes upon it. Instead of bearing the weight on the length of the laminæ, as at the toe, it bears it on the width in such a manner that where we have, say, one lamina at the toe, there are twenty at the quarter. It is not possible to clearly describe this, but Fig. 46 will explain.

These laminæ are attached at the anterior and part of the lateral face of the foot to bone, but for the remaining lateral face and posterior part of the foot they are attached to stout cartilage;* if a line be drawn through the foot separating the osseous attachment of the laminæ from the cartilaginous attachment (see Fig. 49), it will be found that roughly speaking one-half is cartilaginous and one-half osseous; the cartilaginous portion is situated just where elasticity is required, viz., the posterior face of the wall; one function of the lateral cartilages of the foot is to afford an elastic wall attachment to the sensitive laminæ.

A horse's sole carries but little of his weight, only the

* Some of the laminæ are attached to the tendon of the extensor pedis, and the lateral ligaments of the foot joint.

margin which is immediately in contact with the wall assisting. When we remember that the sole is concave, it will be clear that it has some other function than that of weight-bearing to perform; its function is to protect the sensitive sole and pedal bone.

The folding up of the horny and sensitive leaves in the foot, in the manner above described, has another function besides that of merely supporting the weight and rendering the union firm.

It is clear that by folding up this amount of material the surface of the foot is considerably increased. In other words, by this arrangement the foot has been kept within small proportions, without affecting its stability. A book, say of 500 pages, may, by placing one leaf on the other, be made to occupy a bulk represented by a few inches; but if each page be laid out separately on the ground, and made to touch one another, the surface covered will be considerable. This is exactly what occurs in the foot. The horny and sensitive leaves by their singular arrangement increase the surface of the foot, and yet keep it within reasonable bounds. Bracy Clarke, who first had a calculation made as to the increased surface afforded by this arrangement, came to the conclusion that it was equal to $1\frac{1}{2}$ square feet; but Moeller* has estimated that it is equivalent to 8 square feet; whilst Gader's estimate† is $10\frac{3}{4}$ square feet. For safety we will adopt Moeller's number.

The bearing surface afforded by each foot is equivalent to 8 square feet, affording a total area for the pedestals of 32 square feet.

The physiological function of the leaves of the foot is demonstrated by pathological observation. Inflammation of the leaves occurs either through over-work, or through an animal standing too long in one position; in either case they get strained, and resent it. We all know the practical value of exercising horses which from any reason have to

* *Veterinary Journal*, vol. v.

† Quoted by Goubaux and Barriere.

stand up for any length of time, the exercise overcoming the tendency of the laminæ to congestion from continual strain; and the feet not only become cool, but the animal may continue standing for a considerable time if daily exercised. The value of exercise in the treatment of laminitis, first taught us by Mr. Broad, of Bath, is based on the most satisfactory physiological basis.

If any doubt exists as to the function of the laminæ in supporting the weight of the horse's body, we have only to look at the processes which occur in them as the result of disease. Laminitis is often attended by separation of the horny and sensitive laminæ, when the horse's weight being no longer properly supported, the pedal bone under the influence of the animal's weight is actually forced through the sole of the foot.

Anti-concussion Mechanism.—The arrangements which exist to save the foot from concussion are numerous. We have, in the first instance, the highly elastic and india-rubber-like horny frog, the fibro-fatty or plantar cushion, the elastic cartilages of the foot, the elastic posterior wall, and, moreover, the descent of the sensitive foot within its glove, the horny foot.

The descent of the sensitive foot has been as strongly denied as the expansion of the posterior wall, but there is no difficulty in demonstrating it,* and we can see the value of this function. The foot comes to the ground either flat or the frog first; I believe that in the slower paces it comes to the ground nearly flat, but in the faster paces there is no doubt whatever but what the frog comes first to the ground, viz., the posterior part of the foot first, the anterior part last. The frog, from its peculiar physical condition, is not only adapted to prevent the horse from slipping, to give him a grip on the ground, but also to save the foot and leg from concussion; that is the reason why it comes first to the ground. Concussion to the anterior part of the foot is prevented by a slight up-and-down play between the laminæ and the pedal bone, through the medium of the

* See the articles alluded to on p. 358.

extensive layer of elastic tissue found at this part; as the weight comes on the foot, the pedal bone slightly descends, to rise again when the weight is taken off it. As the pedal bone descends, the sole on which it is resting also slightly descends and comes nearer to the ground, which is the reason why the sole is concave instead of flat. The descent avoids concussion, in the same way that it is easier to catch a cricket-ball with a retreating movement of the hand than by rigid opposition.

Much more might be said of practical importance on this subject, but we have other points which press for our consideration.

The Frog.—The function of the horny frog and its peculiar physical features we have already alluded to. The manner in which it protects the important navicular bursa is also no insignificant part of its function. The soft and elastic condition of the horn of the frog has been attributed to certain perspiratory glands which are found in that part of the sensitive frog on either side of the frog stay; how far these actually contribute to the elastic condition of the frog is not clear, especially as the surface over which they are distributed is of very limited area.

The frog is peculiar, inasmuch as it needs for its perfectly healthy condition contact with the ground. It is strange that in this respect two structures situated side by side, viz., the sole and frog, should be so opposed in function. We know practically, that if the frog be kept off the ground, the part atrophies, the heels contract, viz., the foot is rendered smaller, and the frog becomes diseased. This wasted condition of the frog may be restored by pressure, but that pressure must be ground pressure. It is possible by means of a bar-shoe to throw considerable pressure on the frog and heels, but the foot still contracts; it is only when the frog is touching the ground that it continues in a healthy condition, and retains its normal size. Frog pressure is therefore one of the golden rules in shoeing if the frog is to exercise its natural functions.

The Wall.—From what we have previously said, it can

be seen that it is on the wall of the foot where the horse's weight is supported. On examining the horny wall, we find that it is thickest at the toe, thinner at the quarter, and thinnest at the heels. It is thickest at the toe owing to the wear and tear of the foot at this part. As the frog is the first to come to the ground, so is the toe of the wall the last to leave it; and when, as we have seen in studying locomotion, the propulsion is given to the body by the toe of the foot, we can understand how necessary it is to thicken the part here. The toe of the wall appears to grow faster than either the quarter or the heels, but this is more imaginary than real. It is the tendency of the foot to grow *forward* as well as downward which produces the illusion. That the foot does grow forward may readily be determined by experiment, for if we cut or saw a groove in the wall at the coronet, say an inch or so from the heels, that groove will in course of time be carried some considerable distance forward. The exact amount can be determined by observing the obliquity of the horn fibres. The object of the wall becoming thin towards the posterior part of the foot is to allow of the elastic movement which we have described as expansion and contraction.

Two physical conditions have to be provided for in the wall, viz., elasticity of the posterior part, and toughness of the anterior portion. Some of the methods by which the needful provision is made we have spoken of, but here is a general summary of the subject:

The posterior portion of the foot first receives the weight of the body (certainly in all fast paces): the expansion of this part saves it from destruction, and the various provisions which exist are considerably assisted by the fact that the wall is thinner at the heels than elsewhere, and so yields outwards; but besides being thinner the wall of the heel contains more moisture than the wall of the toe, and this moisture ensures its elasticity. The younger the horn, viz., the nearer to the coronet at which the horn is taken, the more moisture it contains, the further away from the coronet the less moisture it contains, and the tougher and more resisting the horn.

Let us observe how perfectly horn of various degrees of moisure, viz., of varying degrees of toughness and elasticity, is provided for in the foot.

1. The anterior part of the wall is longer than the posterior, therefore the anterior is tougher than the posterior, for the reason that the horn is much older at the extremity of the toe than at the heel, and it is further away from the coronet, and therefore contains less moisture.

2. The wall at the heel is some months younger than at the toe; it is thinner, and contains more moisture, therefore it is more elastic, but not so tough.

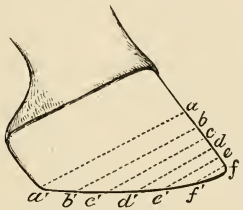

FIG. 47.—DIAGRAM ILLUSTRATING THE AGE OF THE WALL.

a, *b*, *c*, *d*, *e*, *f*, are circles drawn around the hoof parallel to the coronet: in this way we ascertain that the age of the wall at *a* is the same as the heel at *a'*, the age of the wall at *d* corresponds with the age of the quarter at *d'*. Every portion of the ground surface of the wall is of a different age, being oldest and hardest at *f'*, and youngest and most elastic at *a'*.

The age of the wall is, therefore, an important factor in the wear of the foot. The horn of the quarter is older than the horn of the heel, and the horn of the toe older than that of the quarter. This excellent provision for wear admits of that considerable friction between the ground and the toe which occurs during progression, and allows of the expansion of the younger and moister horn of the posterior part. I am not aware that this explanation of the different ages of the wall has ever before had attention directed to it.

The expansion of the wall is aided by the lateral cartilages, which carry outwards the sensitive laminæ, and so

keep them in connection with the horny ones, without which provision a drag on the dovetail arrangement would occur. The fact of the lateral cartilages affording attachment to about half of the sensitive laminæ has been previously mentioned. As the posterior wall contracts the lateral cartilages are carried inwards.

At the heels the wall is turned in to form the bars, which run some distance under the foot towards the apex of the frog. The bars are part of the wall, and their function is the same, viz., to support weight, for which purpose they have the usual dove-tailed sensitive and insensitive laminæ.

The **elastic movement of the foot** must now occupy our attention. The mechanism which brings this about has already been touched on; it only remains for us to briefly describe the changes in shape which the foot undergoes as the result of the body-weight.

When the weight comes on to the foot, it is received by the posterior part of the foot, viz., the posterior wall, bars, frog, and through this the plantar cushion. The elastic posterior wall is pressed outwards by the compressed india-rubber-like frog, and it expands from the coronet to the ground surface for about $\frac{1}{50}$ of an inch; sometimes the expansion at the coronet is not so marked as it is at the ground surface, but in the majority of feet it exists. At the moment of expansion the bulbs of the heel of the foot at the coronary edge sink under the body-weight, and come nearer the ground; and as a result of this, the anterior coronary edge, that corresponding with the toe of the wall, retracts, and the pedal bone slightly descends through its elastic connection with the sensitive laminæ, and presses the sole down with it. Under these conditions the blood pressure in the veins of the foot rises, and the vessels are emptied. When the weight is removed from the foot the bloodvessels fill, the frog retracts, the posterior walls contract and become narrower from side to side, and the bulbs of the heel rise; at the same time the anterior edge of the coronet goes forward, and the pedal bone and sole ascend.

Lungwitz lays stress upon the tense condition of the

coronary edge of the foot at the moment of the greatest weight, and describes it as an elastic ring. Dr. Macdonald,* in this country, who has devoted attention to the vascular mechanism of the horse's foot, considers that the swelling up of the coronary cushion can only be regarded in the

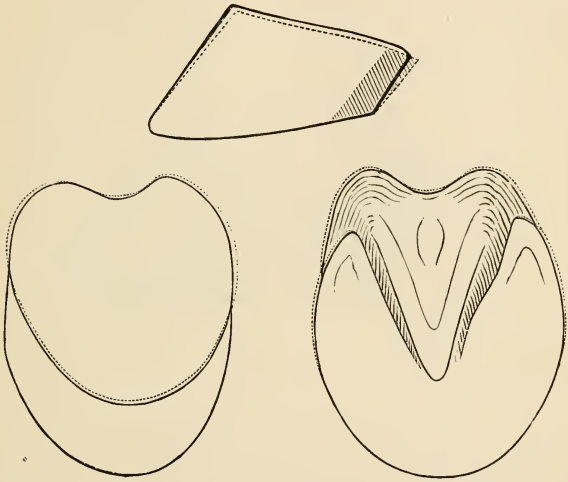

FIG. 48.—DIAGRAMS ILLUSTRATING THE EXPANSION OF THE FOOT.

In the top figure the solid outline indicates the position of the foot at rest: the dotted outline shows the retreat of the coronet, and descent of the heels under the influence of the body weight; the shaded portion of the wall indicates the area of expansion. The two lower figures are after Lungwitz: the left-hand one supposes the observer to be looking down on to the foot; the dotted outline indicates the retreat of the coronet and descent of the heels; the dotted outline of the right-hand figure indicates the expansion of the wall.

light of a powerful hydraulic ligament, which supports the joint under the immense strain to which it is exposed. The value or existence of this hydraulic support has yet to be demonstrated.

Lateral Cartilages.—We have dealt with certain functions

* *Veterinary Record*, No. 145, 1892.

of the lateral cartilages, but it will not be amiss to here summarise our knowledge of their use.

1. They form an elastic wall to the sensitive foot, and afford attachment to the sensitive laminæ.

2. As the foot increases in size the cartilages carry out-

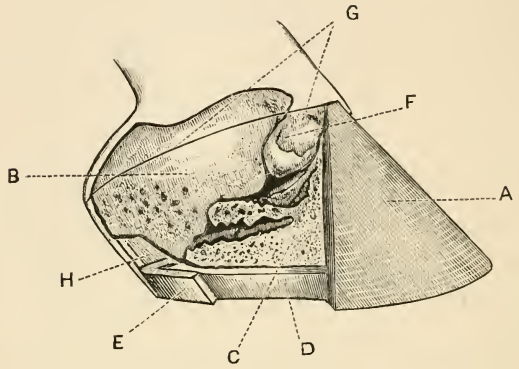

FIG. 49.—PORTION OF THE WALL REMOVED, TO SHOW THE POSITION OF THE RIGID AND ELASTIC SENSITIVE FOOT.

A, wall of the foot; B, the lateral cartilage; G, a line which represents the coronet; C, the pedal bone—the line of union between the pedal bone and lateral cartilage is well seen; F, is a portion of the os corona; D, a portion of the sole exposed by the removal of the wall; E, the heel of the wall left at its plantar surface to show the arrangement of the bar, H, which passes behind and within the lateral cartilage B. The figure, which is accurately drawn from a photograph, is intended to show what an extensive surface the lateral cartilage presents, and the variety of surfaces to which the sensitive laminæ are attached; they cover B, C, and F, the latter in the living animal being the position of the extensor pedis tendon and lateral ligament of the foot, to which the laminæ are attached. Further, the figure shows the division of the internal foot into an elastic and a rigid portion.

wards the sensitive laminæ which are attached to them, and so prevent any disturbance of the union of the horny and sensitive laminæ.

3. Large venous trunks pass through, and close to, the cartilages of the foot, and the movements of the cartilages assist the venous circulation. The function of the lateral

cartilages has light thrown on it by diseased processes. When this elastic cartilage becomes converted into bone, its functions are destroyed, and lameness occurs. I have shown that by a simple operation relief from this lameness may, in a large proportion of cases, be secured, and demonstrated that by surgical interference it is possible to make the horny foot larger, and thereby render it capable of accommodating, without inconvenience to the animal, lateral cartilages which have undergone the process of ossification, and thus increased in size. This operation is based on physiological principles.

4. The object of having elastic cartilages at this part of the foot is to allow of expansion.

Navicular Bursa.—The pedal bone presents a remarkably small articulatory surface, much smaller than the surface of the bone which rests on it. In order to increase this articular surface a sesamoid bone is introduced, known as the Navicular; by this means the corona rests on an articulation which anteriorly is rigid, but posteriorly is flexible. Under this yielding sesamoid bone passes the perforans tendon, and the weight on the bone is supported almost solely by this tendon. I have shown* that the compression to which the navicular bone is thus exposed by the weight of the body from above, and the pressure of the perforans from below, is the chief factor in the production of that serious and common lameness, navicular disease. I do not consider, as is generally believed, that the navicular bone acts the part of a pulley.

When the foot comes to the ground the weight of the body comes first on to the flexible articulation in the pedal joint, viz., the navicular bone and its supporting tendon, the perforans; the corona is then rotated in such a manner that the weight of the body is transferred to the pedal bone, and through this to the laminæ.

Wherever we look in the foot we find the same provision maintained for an elastic posterior and rigid anterior foot.

* *Veterinary Journal*, 1886, 'The Pathology of Navicular Disease.'

Such are the physiological features of the foot which facilitate circulation and destroy concussion. Foot-lameness is only too frequent, but if it were not for the mechanism we have described, it would not be possible for us to work horses for a single day. It is no argument against expansion that it requires delicate apparatus to detect it, owing to its minuteness; small as it is in the slower paces, it yet suffices to convert what would be a rigid, unyielding block into an elastic and yielding one; and at the gallop the expansion must be considerable, probably more than double what it is under ordinary conditions.

Physiological Shoeing.—It is impossible to conclude this chapter on the foot without some mention of what we might term physiological shoeing.

We all recognise the evil of shoeing as strongly as we recognise its necessity. By bearing in mind the functions of the various parts of the foot, we can certainly reduce the evil of shoeing to comparatively narrow limits, and in a few words we will state what constitutes physiological shoeing:

1. The reduction of the wall to its proper proportions, such as would have occurred through friction had no shoe been worn.

2. Fitting the shoe accurately to the outline of the foot, not altering the latter to fit the shoe. Rasping away the crust to fit the shoe not only renders the horn brittle, but is so much loss of bearing surface.

3. Leaving the wall intact, so far as its varnish-like layer is concerned. The practice of rasping the wall for appearance' sake destroys the horn tubes, and allows of so much evaporation from the surface of the foot that the wall becomes brittle.

4. The sole not to be touched by the knife; it cannot be too thick; it is there for the purpose of protection.

5. The bars not to be cut away; they are part of the wall, and intended to carry weight. The shoe should rest on them.

6. The frog to be uncut and left to attain its full growth, which can only occur through resting on the ground. No

frog can perform its function *unless on a level with the ground surface of the shoe.*

7. The pattern of shoe is immaterial so long as it has a true and level bearing, and rests well and firmly on the wall and bars. I believe the simpler the shoe the better, viz., one plain on both ground and foot surface, to be secured with no more nails than necessary, as the nails destroy the horn, and these are not to be driven higher than needful, for high nailing is ruinous to feet.

Such, briefly, are the conditions which fulfil physiological shoeing.

CHAPTER XIX.

THE VOICE.

The voice of each class of animal—horse, ass, ox, sheep, etc. —is so distinctive that we may recognise their presence without seeing them; yet, though the larynx in all these animals differs more or less, the difference is not sufficiently great to offer an explanation of why the sounds it emits are so entirely distinct.

The voice of male and female animals differs in intensity. The wild neigh of the stallion is very different from the neigh of the mare, and the bellowing of the bull is distinctive from that of the cow.

The operation of castration has a remarkable effect on the voice, the neigh of the gelding resembling that of the mare.

In the horse the voice is used during sexual excitement, also during fear or especially loneliness, during pain, anger, and as a mark of pleasure. It is not possible to convey in words the difference in the notes produced, but they are easy to recognise.

The horse is essentially a sociable animal. When he is used to being in the company of others he hates separation, and he shows it by persistent neighing. This is perhaps more noticeable amongst army horses than any others.

The neigh of pleasure is often spoken of as the 'whinny.' The word rather conveys an idea of the sound made.

Sounds which can only be described as screams are often evoked during 'horse-play' and temper, or by mares during œstrum. It is not a scream as we know it in the human

subject, but no other word conveys an idea of its shrillness.

If a horse cries from pain (which is very rare) as during a surgical operation, the cry is a muffled one and short; it is a groan rather than a cry.

The larynx is divided into a respiratory portion and a vocal portion; the latter comprises the region of the vocal cords and their attachment, the former the glottal opening formed by the arytenoid cartilages.

Production of Sound.—If air be forced between the vocal cords so as to cause them to vibrate, sound is produced. The various modifications of that sound are produced in the air-passage anterior to the larynx, such as the posterior nares, the nostrils, and in the horse the false nostril and perhaps the guttural pouch. How far the latter assists in producing the voice is not clear; but it has been considered that it plays some part in the process, though Colin mentions that, when he opened the guttural pouches, the horse's neigh had lost but little, if any, of its ordinary character. I have previously expressed myself that this remarkable pouch is perhaps more intimately connected with the sense of hearing. In the false nostril sounds are certainly produced of an expiratory character, such as the peculiar snort of a frightened or 'fresh' horse. The sacs during these sounds are considerably dilated.

During ordinary respiration, the vocal cords are apart, but when voice is produced, the edges of the cords are approximated and made parallel, so that the rush of air passing between them causes them to vibrate, the tone produced depending on the tension of the cords. If air be forced through a dead larynx, and the tension of the cords increased and decreased, a sound remarkably like a neigh may be produced.

The ventricles of the larynx, cavities of the mouth, nose, and pharynx, act as resonators, being filled with air. The ventricles of the larynx also allow of the free vibration of the vocal cords; they are very large in the horse and howling monkeys.

The cartilaginous box, the larynx, undergoes at its glottal opening certain changes in shape during inspiration and expiration. During ordinary inspiration it slightly opens, and the vocal cords, which were towards the centre of the tube, retire towards the side. During expiration the glottal opening becomes smaller and the cords approximate.

Movements of the Larynx.—These movements are carried out by certain muscles in connection with the cartilages of the larynx and vocal cords, and the muscles may be divided into those which dilate the cavity and those which close it. The sole dilator is the crico-arytenoideus posticus, a muscle of considerable power, and strengthened by tendinous fibres in its substance. Its function is to lift the arytenoid cartilage upwards and outwards, more especially during forced respiration, when the glottis is dilated to its utmost. It is *the* muscle of the larynx, and paralysis of it causes laryngeal 'roaring,' owing to the immobile arytenoid cartilage being drawn into the glottis, instead of being lifted up out of the way of the incoming air. The paralysed vocal cord takes no part in the production of the sound, which, it is to be noticed, is almost invariably an inspiratory one.

The larynx having been dilated, it is then closed partly by its elastic recoil, but also through the medium of the muscles antagonistic to the dilator, viz., the constrictors, or, more correctly, the adductors, of which there are four on either side, viz., the arytenoideus, thyro-arytenoideus anticus and posticus, and crico-arytenoideus lateralis. By the contraction of these muscles the glottis is closed, the arytenoid cartilages depressed, their glottal surfaces closely applied, and they also bring the vocal cords together, or nearly so, forming a simple slit between them.

The vocal cords, lying in close apposition to the thyro-arytenoideus posticus muscle, are relaxed by a contraction of this muscle, which approximates the arytenoid and thyroid cartilages; whilst the crico-thyroid places the cords on the stretch, or renders them tense by the manner in which it rotates the cricoid on the thyroid cartilage. The

vocal cords by being stretched and relaxed produce the pitch of the note emitted; the pitch of the note produced thus depending on the tension of the cords.

The nerve supply of the larynx is peculiar, and of considerable practical interest. Sensation to the mucous membrane, and portion of the epiglottis and glottis, is supplied by the superior laryngeal division of the tenth nerve. Motor power is supplied to all the muscles of the larynx, excepting the crico-thyroid, by the inferior laryngeal or recurrent nerve, which is given off from the pneumogastric in the chest: that on the right side winding around the axillary artery and passing up the neck supplies the right larynx, whilst on the left side it passes around the aorta and returns up the neck, in its passage being exposed to aortic pressure and any pressure arising from diseased bronchial lymphatic glands, through the substance of which it passes; it thus reaches the left side of the larynx and supplies it with motor power. It is this branch of nerve which supplies the muscles implicated in 'roaring,' especially, of course, the inspiratory muscle of the larynx—the crico-arytenoideus posticus.

The crico-thyroid muscle in the horse is supplied with motor power by the first cervical nerve; this, according to the experiments of Moeller, is beyond all doubt.* We know that in the most acute case of laryngeal paralysis this muscle is quite sound. Chauveau and others have shown that the spinal accessory supplies the superior laryngeal division of the tenth nerve with motor fibres.

Swallowing may be excited by touching the vocal cords, but especially the anterior extremity of the arytenoid cartilages; the adductor muscles then close and depress the glottis, and the free mucous membrane of the ary-epiglottic folds, together with the epiglottis, close the entrance into the larynx. The presence of the arytenoid cartilage is not essential to swallowing, or, rather, its presence is not necessary to prevent food passing into the trachea.

Neighing in the horse is produced by an expiration,

* Fleming's 'Roaring.'

whilst the **braying** of the ass is both an inspiratory and expiratory effort. In both cases the sound partly comes through the mouth.

In the ox, sheep, and goat there are no ventricles in the larynx, and only rudimentary vocal cords. In the ass the ventricles are very large.

Yawning is a deep, slow inspiration, and though the horse opens the mouth and slightly crosses the jaws, I am not certain whether the whole of the air or only part of it passes by the mouth.

Sneezing and coughing are expiratory efforts, the former occurring through the nostrils, the latter through the mouth; but in both yawning and coughing the long soft palate of the horse must be raised to allow the air to pass into the mouth.

CHAPTER XX.

GENERATION AND DEVELOPMENT.

The seminal fluid is secreted by the testicle, and constitutes the fecundating material of the male. As discharged from the urethra, it is mixed with the secretion of the prostate and vas deferens. It is not known what part the accessory secretions play, but they appear to be essential to fertility.

The spermatic fluid is alkaline or neutral in reaction, of gelatinous consistence, and was found by Lassaigne, who examined the material taken from the vesiculæ seminalis of the horse, to contain a large quantity of water, an abundance of a substance termed by him spermatin, mucus, soda, chloride of sodium, and phosphate of lime. Colin describes the spermatic fluid of a bull after standing to consist of two parts—the upper colourless and transparent, the lower stratum milky and opaque. He regards the former as prostatic fluid, the latter as spermatic. More recent analyses of this fluid show it to contain serum and alkali albumin, nuclein, lecithin, cholesterine, fat, leucin, tyrosin, kreatin, inosit, sulphur, alkaline earths, and phosphates.

The essential element of the spermatic fluid is the spermatozoa, without which the fluid is not fertile. They are developed in the seminal tubes of the testicle from the so-called spermatoblasts. These are projections from the wall of the tube, which, when ripe, leave the wall, and are carried along in the fluid. They exhibit spontaneous movement, the long tail moving from side to side, by which means the organism is propelled when placed in the body

of the female. The vitality of the spermatozoa is considerable under suitable conditions; and when placed in the body of the opposite sex they have been found very active seven or eight days after copulation. Colin has found them in a similar state in the vesiculæ seminales eight days after castration. The spermatozoa are readily killed. Colin says that those of the ox, horse, and carnivora are killed immediately by ordinary or acidulated water, glycerine, etc.

The prostatic fluid precedes the spermatic in ejaculation, and in stallions and bulls, when excessive daily demands are made, the fluid ejaculated is largely prostatic and infertile.

The testicular products of hybrids, such as the mule, are said to be devoid of spermatozoa.

The act of copulation consists in the introduction of the penis of the male into the vagina of the female. With some animals, as in the dog, the introduction is facilitated by the presence of a bone in the substance of the penis; but in all animals the penis has to become erect and larger before it is fit for penetration.

The **Phenomena of Erection** is produced by a gorging of the vessels of the penis, caused by a dilatation of the arteries, increased blood supply, and pressure on the veins. This is brought about by the nervi erigentes, the fibres of which contain both dilator and constrictor nerves for the walls of the bloodvessels. An erection centre also exists in the spinal cord, normally under the control of the vaso-motor centre in the medulla, though it may act independently of it, as in persistent erection after laceration of the cord. The stimulation of the centre in the medulla may even at the moment of death lead to erection and ejaculation. Colin has observed this in stallions destroyed by section of the medulla, injuries to the head, or even simply by bleeding. The emptying of the bladder and evacuation of the contents of the intestines, in horses destroyed by shooting through the head, is a regular accompaniment of this mode of death, and the same process which empties

the bladder and elongates the penis of the castrated animal, no doubt produces what Colin has recorded of stallions.

The influence of the cerebrum on the mechanism of erection, viz., in stimulating the centre in the cord and medulla, is well known.

The first portion of the penis which receives the excess of blood in erection is the corpus cavernosum; the spongiosum and glans are not fully erect in the stallion until the penis is introduced into the vagina; at the moment of ejaculation the glans swells enormously, apparently to cover or grasp the os uteri. The blood sent to the penis for the purpose of erection is practically imprisoned by the compression exercised by the muscles of the perinæum on the veins of the part, and this mechanism further maintains the blood pressure.

If the nerves of the penis be divided in the horse, erection is impossible, though desire may be intense. Gunther's and Colin's experiments have placed this beyond doubt.

Though the organ in the horse assumes such considerable proportions, in the bull this is not so marked. The penis in this animal comes to a narrow point without any of the swelling observable in the stallion. In the ram, also, the penis is narrow and pointed, and the peculiar vermiform appendage at its extremity appears essential for successful impregnation, for if removed the animal proves sterile.

Sexual Intercourse is of short duration in the majority of animals, excepting the dog and pig. Colin places it at 10 to 12 seconds for a vigorous stallion; it is exceedingly rapid in the bull and ram, probably from the peculiar shape of their intromittent organ.

The spermatic fluid is forced into the vagina, or even directly into the uterus; the peculiar termination of the urethra of the horse, and the bulbous enlargement of the glans during the act of coition, would rather point to the fluid in this animal being directly passed, at any rate to some extent, into the os uteri, and the pointed penis of the bull and ram makes it nearly certain that much of the fecundating fluid passes directly into the uterus.

At the moment of intercourse, the uterus becomes erect, and the introduction of the male element into it is assisted by the aspiration following its subsidence. It would appear necessary in the lower animals for the fluid to pass into the neck of the uterus, and there is probably a great deal to say in favour of the common practice of preventing the mare from straining immediately after copulation, and thus rejecting the spermatic fluid.

The actual mechanism of ejaculation is produced by the contraction of the vesiculæ seminales, and probably of the vasa deferentia, through the reflex action of the ejaculation centre in the lumbar and sacral portions of the cord; by this means the seminal fluid is forced out of the vesiculæ into the urethra, and by means of the muscles of the perinæum is forcibly ejected from the urethra.

The amount of seminal fluid ejaculated by the stallion and bull is estimated by Colin at 770 grains to 930 grains.

The Ovum.—The ovaries prepare the female element, the ovum. The ovum is exceedingly small; it is contained in a thick envelope, the zona pellucida, within which is the yelk, and at one part of the yelk is the germinal vesicle; within the vesicle is the germinal spot. When the ovum is about to ripen, it passes from the periphery of the gland towards the centre and undergoes certain changes, becoming large through the accumulation of fluid within the Graafian follicle; it now passes to the surface of the gland once more, preparatory to bursting.

As the ova ripen, changes take place in the system of the animal, known as 'heat' or 'rutting.' It manifests itself by uncontrollable sexual desire, which comes on at fairly definite periods, and lasts for a certain number of days. In the lower animals it is not accompanied by anything approaching the menstruation in the human female. Although slightly blood-coloured discharges have been observed in animals, we may fairly say that menstruation proper is not a normal occurrence, due probably to the fact that neither horses, cattle, nor pigs have anything of the nature of a uterine decidua.

The ripened bladder-like Graafian vesicle comes to the surface of the ovary and bursts; but before this occurs, the fimbriated expansion of the Fallopian tube has embraced it, the ovum passes into the canal, and, by means of the cilia which line it, is impelled towards the uterus. In the Fallopian tube it meets with the male element, and impregnation of the ovum occurs in a manner which will be presently described. Should the fimbriæ of the Fallopian tube fail to grasp the vesicle, the ovum falls into the abdominal cavity and there perishes, or, if it has already met with the male element, an extra-uterine fœtation occurs.

The period of heat manifests itself at different times: the mare is 'in season' during the spring and summer, the period lasting two to four days, and recurring every three or four weeks; during the interval the male is not accepted. The cow is much the same as the mare; sheep take the ram in the autumn.

The male is attracted to the female by a peculiar smell, which can even be detected by the former at some considerable distance.

The number of ova discharged at each period varies: generally one for the mare and cow is the rule, though two may be discharged; one to four for the sheep; whilst the pig may discharge ten or more ova at one time.

The **Period of Puberty**, or that time in the animal's life when it is capable of procreation, has been put at 3 years for horse and ox, and 12 months for the sheep; the females may conceive at an earlier period than this—in fact, commonly do. A mare may conceive between 12 months and 2 years, a cow 12 to 18 months, sheep and goat 8 to 12 months. The use of immature mares for breeding stock is the explanation of a great deal of the worthless material in the shape of horseflesh which may be seen in this country. In my opinion, neither mare nor horse is fully developed, mature, or fit for procreation until 5 years old.

The advent of maturity is marked by certain changes in

form, particularly in horses. They lose their awkwardness, the outline of the frame becomes more consolidated and in greater unison. In the male the neck becomes thick and curved, the voice deepens, and the whole appearance denotes life and vigour; the temper is usually irritable and uncertain, and often extremely vicious.

The age at which procreation ceases is not known. Fleming* says that mares have been known to produce foals at 28, 32, and 38 years of age, and it is certain that some of our best stallions are well advanced in years.

Changes in the Ovum.—Before impregnation the germinal vesicle and spot undergo changes, and the place of the vesicle is taken by a spindle-shaped body; at each end of the spindle the elements of the yelk arrange themselves in the form of a star. The peripheral pole of the spindle projects outside the wall of the ovum, and is cut off; the remaining pole is termed the female pro-nucleus.

The ovum is impregnated in all probability in the Fallopian tubes or tube. The spermatozoa passing through the yelk envelope, or zona pellucida, and forming the male pro-nucleus, which passes deeper into the ovum, and approaching the female pro-nucleus, causes it to become active. The change which now follows is segmentation of the germinal vesicle, which divides and subdivides into an indefinite number of small bodies. Next, the yelk in which the small bodies of the germinal vesicle are distributed begins to become segmented in twos, fours, eights, etc., until the whole surface of the yelk is converted into a mulberry-looking mass, consisting of minute spherules, termed vitelline spheres. These now pass to the wall of the vitelline membrane, and arrange themselves on its inner surface, while the central portion of the ovum becomes clear and transparent. The vitelline spheres which have thus passed to the wall arrange themselves into a kind of membrane termed the blastodermic or germinal membrane. The cells of the germinal membrane accumulate at one point and form an opaque spot, the germinal area, which in

* 'Veterinary Obstetrics.'

time becomes pear-shaped, and corresponds to the direction of the future embryo.

At the posterior part of the germinal area the primitive streak appears, and soon becomes a groove termed the primitive groove.

Leaving the ovum for the moment, we must describe the changes which have occurred in the blastodermic layer which was left on the inside of the vitelline membrane. It is found that this layer divides at first into two, and then into three layers. The outer, called the ectoderm, epiblast, or serous layer, grows the central nervous system and epidermal tissues, including hoof. The inner or lower layer is termed the endoblast or hypoblast, and grows the intestinal canal and the glands opening into it. The middle layer, or mesoblast, forms the bloodvessels, and constitutes a part termed the area vasculosa; it also grows the muscles and skeleton, generative and excretory organs.

Returning to the primitive groove, it is found that in front of it is formed another groove, the medullary, which, extending back and opening out, encloses the primitive groove and causes it to disappear. The growth of the medullary groove has given rise to a part termed the area pellucida, surrounded by an opaque surface, termed the area opaca. In the pellucid area is formed the embryo. The medullary groove grows from the epiblast; from either side of the groove rises up a structure termed the lamina dorsales, which, growing over the groove, meet, and thus form a canal termed the neural canal; in this is developed the brain and spinal cord.

Underneath the medullary groove is formed from the mesoblast a cord termed the notochord, from and around which are developed the vertebræ. From another portion of the mesoblast is formed the pleuro-peritoneal cavity. Two important structures appear at this time, developing from one or other of the layers into which we have seen the blastodermic membrane is divided. By the union of certain layers of the mesoblast with the epiblast a structure termed the somatopleure is formed, and from a layer of the

mesoblast with the hypoblast is formed the splanchnopleure. From the somatopleure is formed the skin, muscles, and bloodvessels; from the splanchnopleure is formed the intestinal canal.

The embryo now undergoes a change in shape, for at each end an inflection or tucking in of the layers surrounding it occurs. These inflections are spoken of as the head and tail fold. As this folding under the body occurs, the embryo (ventral surface downwards) is raised higher and higher, so that at last it rests at the future umbilicus on a narrow stalk or pedicle, termed the vitelline duct, which communicates with a sac outside the body of the embryo termed the umbilical vesicle; in the body of the embryo the vitelline duct communicates with the primitive intestinal canal.

From the splanchnopleure is now developed the heart, then the aorta, from which is given off several vessels termed omphalo-mesenteric arteries, which form, by passing through the vitelline duct, a vascular network within the umbilical vesicle, and from here arises the omphalo-mesenteric veins, which return to the body of the embryo by the vitelline duct, and terminate in the heart.

This is the primary embryonic circulation. The umbilical vesicle is furnishing the embryo with nutriment, but this does not last for long, for when the placental circulation is established, the umbilical vesicle has no longer any function to perform, and it gradually disappears.

We must now describe the formation of two sacs which are found outside the body of the embryo, which at this time are destined to perform important functions, and in their arrangement are different from those occurring in the human subject.

The **Amnion** is formed from the somatopleure, growing over the embryo from all sides, meeting, and then forming a cavity termed the amniotic, which eventually contains a quantity of fluid in which the embryo resides. The amnion surrounds the duct of the umbilical vesicle, and we may describe it as terminating at the umbilicus, where

it eventually forms the amniotic portion of the cord. The liquor amnii is an albuminous alkaline fluid, yellowish in the early period of gestation, reddish toward the end of it, probably due to discoloration with meconium. It consists of albumin, mucin, globulin, sugar, urea, lactic acid, keratin, calcium sulphate, phosphates, and sodic chloride; it contains also portions of hoof, epithelium, etc.

Gurlt, quoted by Fleming, puts it at 2 lbs. 12 ozs. at the twenty-first week of pregnancy in a mare, and at the fortieth week the amniotic and allantoic fluids amounted to 19 lbs. The function of this fluid is protective to mother and fœtus, and during parturition it dilates the os and lubricates the passage.

The **Allantois** is formed from the splanchnopleure, growing out from the body of the embryo at the future umbilicus. As it grows from the umbilicus it spreads out, and in the mare completely envelops the amnion, though in ruminants it only partially envelops it. The part of the allantois within the body of the embryo becomes the bladder, and this is brought into communication with the allantois outside the body, by means of the urachus, which passes through the umbilicus; the urine from the bladder passing through the urachus, distends the allantoic sac with this fluid. The outgrowth of the allantois is to establish communication with the vascular covering of the embryo, the chorion; in the mare it lines the chorion as well as being reflected over the amnion.

The allantoic fluid of the mare is at first colourless or turbid, but later becomes brown; it contains albumin, sugar, urea, lactic acid, phosphate of lime, soda, and magnesia, and in the cow allantoic acid.

Floating in the allantoic fluid of the mare are certain peculiar bodies of a brownish colour, termed **hippomanes**; they contain much oxalate of lime. Some of these bodies are attached to the wall of the allantoic sac. Their use is unknown.

In ruminants the allantois is smaller, and only partially envelops the amnion; it is attached to the chorion between

the horns of the uterus. The urachus communicates with the allantois as in the mare; but, unlike the latter, it is constantly found to be pervious at birth.

Surrounding both these sacs we have the **Chorion**, which forms the connection, through the medium of the umbilical cord, between the mother and embryo. It is developed from the outer or vitelline covering of the embryo, and important differences are observable between its arrangement in the mare and in ruminants. In the former the chorion is attached all over the inner surface of the uterus, excepting at the os; in ruminants the chorion is attached to the uterus by cotyledons, dotted here and there over the surface, about 60 or 80 in number; while in the pig the placenta is like that of the mare.

The development of the chorion from the vitelline layer occurs by tufts of vessels forming on its exterior, either all over as in the mare, or dotted here and there as in the cow. These villi project themselves into the mucous membrane of the uterus, not through the medium of a decidua, as in the woman, but directly into the wall of the uterus, as solipeds and ruminants possess no decidua. As the umbilical cord forms the connection between the embryo and the chorion, a perfect communication is kept up between the mother and embryo, not by the direct passage of blood from mother to fœtus, but through the capillary walls only, for the vessels of the one do not directly communicate with the vessels of the other.

The **umbilical cord** is composed of two portions: an amniotic, which is nearest the fœtus, and an allantoic, which is next the chorion and outside the amniotic cavity; this is the arrangement in the mare. The umbilical cord in ruminants has no fold of allantois, owing to the anatomical difference in the arrangement of this sac, but it directly enters the chorion from the amnion. In both classes of animal the cord is made up of a gelatinous material, known as 'Wharton's jelly,' containing the umbilical arteries and veins passing to and from the chorion. The cord is about

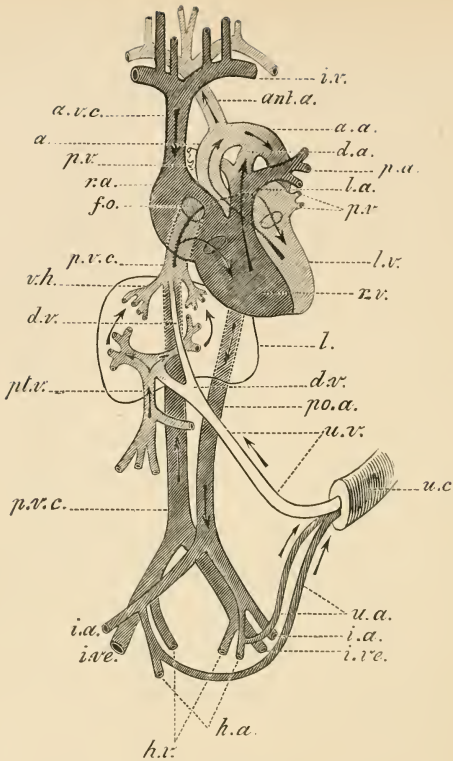

FIG. 50.—DIAGRAM OF THE FŒTAL CIRCULATION. (ELLENBERGER–BONNET.)

u. v., umbilical vein ; *d. v.*, ductus venosus ; *pt. v.*, portal vein ; *l.*, liver ; *v. h.*, hepatic veins ; *p. v. c.*, posterior vena cava ; *r. a.*, right auricle ; *f. o.*, foramen ovale ; *r. v.*, right ventricle ; *p. a.*, pulmonary artery ; *d. a.*, ductus arteriosus ; *l. a.*, left auricle ; *l. v.*, left ventricle ; *a.*, the aorta ; *a. a.*, arch of aorta ; *ant. a.*, anterior aorta ; *i. v.*, innominate veins ; *a. v. c.*, anterior vena cava ; *po. a.*, posterior aorta ; *i. a.*, illiac, artery ; *h. a.*, hypogastric artery ; *u. a.*, umbilical arteries ; *i. ve.*, illiac veins ; *h. v.*, hypogastric veins ; *u. c.*, umbilical cord. The diagram actually represents the fœtal circulation in ruminants : to make it applicable to the horse the ductus arteriosus (*d. v.*) must be supposed to be removed, the whole of the blood then traverses the liver by the union of the umbilical vein (*u. v.*) with the portal vein (*pt. v.*). The arrows indicate the course taken by the blood : observe how the stream entering the right auricle divides, part passing into the right ventricle, and part into the left auricle through the foramen ovale (*f. o.*).

3 feet in length, and the amniotic portion is twisted very much like the strands of a rope.*

We have traced the development of the ovum from the period of impregnation to the development of the primary circulation and investing membranes. It is not our intention to follow out the development of the various parts of the body, until the fœtus is completely formed, as ample information on these points can be obtained in works on anatomy and embryology.† We will here only mention the peculiarities of the fœtal circulation, as these are of physiological interest.

Fœtal Circulation.—The blood of the fœtus, returning from the placenta in a purified condition, passes by means of the umbilical vein to the umbilicus, then turns and runs along the floor of the abdomen, reaches the liver, and opens into the vena porta; from the union of the umbilical and portal veins, a single vessel results, which breaks up in the liver, and the blood passing through this gland, reaches, in course of time, the posterior vena cava through the medium of the hepatic veins. So that in the fœtal circulation of the horse the whole of the blood first passes through the liver. (See Fig. 50.)

In ruminants the umbilical vein on reaching the liver joins the vena porta, from which a canal—the ductus venosus—takes a portion of the blood direct to the posterior vena cava; the other portion, traversing the liver through the hepatic veins, eventually reaches the posterior vena cava; from here in both animals it passes to the right auricle of the heart, where it meets with the blood which has been circulating through the head, neck, and fore extremities. Here occurs a remarkable change characteristic of the fœtal circulation in all animals: that portion of blood which reached the right auricle by the posterior cava divides;

* To Fleming's 'Veterinary Obstetrics' I am indebted for the account of the masterly foreign researches on the formation of the membranes in solipeds and ruminants.

† The development of the ovum and the various parts is fully described in Chauveau's 'Anatomy' (Fleming), and in Fleming's 'Veterinary Obstetrics.'

part passes from the right auricle into the left auricle through a foramen in the auricular septum, known as the foramen ovale; from the left auricle it passes into the left ventricle, and from here to the aorta, and thence over the body, especially to the head and neck; that portion of blood which reached the right auricle by the anterior cava, passes into the right ventricle in conjunction with the balance of the blood received by the posterior cava, thence into the pulmonary artery, a small portion passing on to the lungs and behaving as in the adult, whilst the major portion passes from the pulmonary artery direct into the aorta by means of the ductus arteriosus, and is distributed by means of the aorta to the posterior part of the body. From the external iliac arteries arise the umbilical arteries, which run along the sides of the bladder, pass out at the umbilicus, traversing the substance of the cord to the placenta, where the impure blood it conveys becomes revivified by the maternal placenta, and in a purified condition it returns once more to the body of the fœtus by the umbilical vein.

Thus it will be seen that the blood circulating in the fœtus is a mixture of arterial and venous, arterial up to the liver, where it mixes with the portal; another mixture occurs in the right auricle, but the greater part of that blood, as we have seen, after performing work in the anterior extremities, is sent by another channel to assist in the nutrition of the posterior extremities, whilst the purest blood in the body is principally directed to the head, which needs it the most.

After birth the circulation changes: the ductus venosus closes, the septum in the auricles becomes filled in, the ductus arteriosus is obliterated, the umbilical arteries become the lateral ligaments of the bladder, whilst the umbilical vein becomes the round ligament of the liver.

The **Duration of Pregnancy** for the mare is about 11 months, though it may vary within wide limits; for the cow, about 9 months; sheep and goat, 5 months; pig, 4 months; and bitch, 2 months.

Among the changes which the uterus undergoes after

impregnation may be mentioned the great increase in the elements of the muscular wall, enlargement of the broad ligaments of the uterus, and the formation in the mucous membrane of depressions, or 'crypts,' in which are lodged the villi of the chorion.

The **Nutrition of the Embryo** is in the first instance carried out by the umbilical vesicle; later, when the membranes are formed, and connected with the interior of the uterus, nutrition is carried on by the interchange of material occurring in the villi of the chorion, and the capillary vessels surrounding the follicles or crypts in the uterine mucous membrane. The capillary vessels of mother and fœtus here come in contact, though there is no communication whatever between them; carbonic anhydride passes through the vessels from the fœtus to the mother, and in return the vessels of the latter give up oxygen to the fœtal villi, by which it is conveyed to the umbilical vessels, and so enters the body of the fœtus.

Uterine Milk.—If the villi of the chorion be separated from the tubular depressions of the mucous membrane of the uterus, a milky fluid can be expressed, known as uterine milk. This is particularly observable in separating the fœtal and maternal cotyledons.

Uterine milk is of a white or rosy-white colour, creamy consistence, and contains proteids, fat, and a small proportion of ash. Examined microscopically it is found to contain globules of fat, leucocytes, and rod-like crystals of albumin-crystalloids, besides structureless masses of proteid containing chromatin.* The use of the fluid is described by this authority as for the nourishment of the epithelial cells of the chorion.

Parturition.—The fœtus having reached its full stage of development, changes of an obscure nature take place, which lead to it being expelled. Preparatory to this process the fœtus changes position; for, from lying on its back on the floor of the mare's abdomen, with its chin on its chest, the fore-legs bent at the knee, and the hind-legs in

* Ellenberger, 'Physiologie.'

the largest of the two cornua, the fœtus now assumes first a lateral position, and lastly an upright one, by which the fœtal and maternal spines are brought nearer together. To assume this position, the fœtus has had to make a complete revolution; it is now brought with the muzzle and fore-legs in the direction of the pelvis, and the dilatation of the os uteri follows. In the cow the fœtus lies on its back on the floor of the abdomen as in the mare, but lies somewhat crooked, viz., the head inclining towards one side, and the hind extremities towards the other; in all other respects it resembles the mare. The alteration in the position of the fœtus does not occur through its own movements, but by the contraction of the uterus; on the other hand, the stretching of the limbs is the result of fœtal movement.*

The dilatation of the os is assisted by the amniotic and allantoic fluids; each contraction of the uterus is accompanied by a pain; the pains last from 15 to 90 seconds, and the interval between them is from 2 to 4 minutes.

The mare is remarkable for the rapidity with which delivery is effected; ruminants, on the other hand, are often very slow, and in labour for hours. The rapid delivery of the mare is accompanied by a complete separation of the chorion from the uterine walls; this is the explanation why any difficulty in foaling invariably sacrifices the life of the foal. In ruminants, on the contrary, the circulation between the mother and fœtus is kept up to the last by the gradual separation of the cotyledons, so that, though calving may be delayed several hours, the calf may, and commonly is, born alive.

The contractions of the uterus occur through a centre in the lumbar portion of the cord; it is not under the control of the will, and has the power of acting even though the animal be unconscious.

Mammary Secretion.

As the period of parturition approaches the mammary glands become swollen, owing to the active changes occur-

* The description of the change in the position of the fœtus preparatory to birth is taken from Ellenberger's 'Physiologie.'

ring in them, culminating in the production of milk at the birth of the young animal.

The earliest milk is termed the **Colostrum**. It is a peculiar yellowish-white fluid, of alkaline reaction, sweetish taste, and remarkable for the amount of proteid it contains; for instance, in the cow, the colostrum contains 15 per cent. of proteid, whilst the normal milk only contains 4 per cent. to 5 per cent.

If the fluid be examined microscopically, it is found to be filled with bodies termed 'colostrum corpuscles.' These are large granular corpuscles filled with fat, which has not yet escaped from the parent cell.

The use of colostrum is to act as a natural purge, and so clear out the intestinal canal of the young animal.

Milk.—This follows the secretion of colostrum. It is a slightly alkaline fluid, soon showing an acid reaction, with a specific gravity in the cow of 1028 to 1034. The following analysis of cow's milk and colostrum from the same animal is given by Halliburton:

	Milk.	*Colostrum.*
Water	84·28	78·7
Solids	15·72	21·3
Casein	3·57	7·3
Albumin	·75	7·5
Fat	6·47	4·0
Lactose	4·34	1·5
Salts	·63	1·0
Specific gravity	1028-1034	1046-1065.

The same authority also quotes analyses of the milk of other animals:

	Mare.	*Sheep.*	*Ass.*
Water	92·5	18-24	90·5
Solids	7·5	15-17	9·5
Casein	1·3	4·7	1·7
Albumin	·3		
Fat	·6	4-8	1·4
Lactose	4·7	3·4-6	6·4
Salts	·3	·6	

The proteids of milk are casein (which clots on the

addition of the rennet ferment) and ordinary milk albumin. Milk acted upon by rennet is divided into clot and whey. The casein of mare's milk is more like human than cow's casein.

If milk be microscopically examined, it is found to be filled with minute oil globules, which form in the milk a perfect emulsion, and so never run together. After the fluid has stood some time the fat globules rise to the surface as cream, though still forming an emulsion. The fat in milk consists of several fatty acids. If the fat be liberated from the globules by beating, butter is formed, consisting of 68 per cent. of palmatin and stearin, 30 per cent. of olein, and 2 per cent. of specific butter-fats (Halliburton).

The sugar of milk is known as lactose; the salts of milk have been dealt with on p. 18.

CHAPTER XXI.

GROWTH, DECAY, AND DEATH.

Growth.—The young of the herbivora very rapidly shake off the helpless condition in which they first find themselves in this world. This is largely due to the fact that they are born with a nervous system in a high state of development; in the course of a few hours they learn to stand and walk, and in a day or two can skip and run. The young animal, moreover, is born in full possession of its senses, such as sight, touch, hearing, smell, taste, and with an amount of intelligence which nearly, if not quite, equals its parent; it practically has nothing to learn but obedience to man.

Not only is the nervous system in an advanced condition, but also the locomotor: the legs of the foal are remarkably long, some of the bones being nearly their full length, though, of course, not of their full weight; such joints as the knee and hock are nearly their full size. We can understand the reason of this development of the limb from what we have previously said, and the length of leg in the foal is undoubtedly for the purpose of enabling the animal to reach the mammary gland.

The limb, however, is only partially developed; from the knee and hock to the ground it is nearly the length of the adult; from the knee and hock to the elbow and stifle it is decidedly below the adult; whilst from the elbow to the withers, and the stifle to the croup, the body has a considerable amount to grow. It has been said, and the statement appears to be true, that the future height of the foal

may be ascertained by measuring the fore limb from the fetlock to the elbow and multiplying it by two.

Table Showing the Length of the Bones of the Limbs of the Foal and Adult Horse.

	Adult Horse.	*Foal of Six Weeks.*	*Difference.*
Scapula	15 in.	$8\frac{1}{4}$ in.	$6\frac{3}{4}$ in.
Humerus	12 in.	8 in.	4 in.
Radius and ulna	18 in.	12 in.	6 in.
Knee-joint	$3\frac{1}{2} \times 3\frac{1}{2}$ in.	3×3 in.	$\frac{1}{2}$ in.
Metacarpal	$9\frac{1}{2}$ in.	$8\frac{3}{4}$ in.	$\frac{3}{4}$ in.
Suffraginis	$3\frac{1}{2}$ in.	3 in.	$\frac{1}{2}$ in.
Femur	17 in.	$10\frac{1}{2}$ in.	$6\frac{1}{2}$ in.
Tibia	$13\frac{1}{2}$ in.	$9\frac{1}{2}$ in.	4 in.
Calcis to metatarsal bone	6 in.	5 in.	1 in.
Metatarsal	11 in.	10 in.	1 in.
Suffraginis	$3\frac{1}{2}$ in.	3 in.	$\frac{1}{2}$ in.

The hind quarters of the foal are in a more advanced state of development than the fore; the shoulders are very oblique, the chest contracted and shrunken-looking, and neither contains much muscle. The oblique position of the scapula is due to the weight of the body on the limbs, the weakness of the muscles at this part allowing the angle formed by the scapula and humerus to be considerably closed, and the shoulder joint to bulge.

The head of the foal is prominent over the brain, and depressed over the nasal bones; the hair is fully developed, that of the mane being scanty, and of the tail curly; whilst the colour of the body is light of its kind.

The rate at which the foal increases in weight, and other circumstances connected with its nutrition, were made the subject of inquiry by Boussingault.* He found that the mean weight at birth was 112 lbs., that during the first three months the daily increase in weight was 2·2 lbs.; from three up to six months the daily increase was 1·3 lbs., and

* Quoted by Colin.

from six months up to three years of age the increase was at the rate of ·7 lb. per diem.

With calves, according to Torcy,* the mean weight at birth is 77 lbs., the daily increase during the first year is 1·5 lbs., during the second year 1·5 lbs., during the third year 1·43 lbs., during the fourth year 1·32 lbs.

With sheep the daily increase in weight is still more rapid: a lamb will in ten days gain 50 per cent. on its original weight, will double its weight at the end of the first month, and triple it at the end of the second.

Swine present, however, the most rapid increase in weight, for, according to the authorities quoted, a pig will increase 20 per cent. in its weight per diem during the first week, and up to the end of the first year is adding ·44 lbs. daily to its body weight.

The growth of the body implies an increase in weight and height; from what we have said respecting the limbs, it may be judged that the amount of growth of each part is not the same: the eyes, ears, brain, kidneys, and liver grow less rapidly than the other parts, owing to their comparatively large size at birth; the greatest increase is in the skeleton and muscles, and the rate of this increase we have just alluded to; the least increase is in the eyes and the ears, and the limbs below the knee and hock.

But few observations have been made on the rate of growth. Percival† many years ago drew up a table, which he considered very imperfect, as to the rate at which some horses of his regiment grew, from which he showed that the increase in height between 2 years and 3 years was on an average one inch, between 3 years and 4 years one-third of an inch, and between 4 years and 5 years one-third of an inch. Of 35 two-year-olds, 2 did not grow in the year; of 144 three-year-olds, 17 did not increase in height during the year; of 48 four-year-olds, 7 did not grow during the year; and of 11 five-year-olds, only 9 grew during the year.

These numbers are too small to generalize from; there

* Quoted by Colin.

† 'Lectures on Form and Action.'

can be no doubt that many horses grow much more than two-thirds of an inch between three and five years old. It is probable that many grow up to their sixth or seventh year.

During the time the young animal is receiving its mother's milk, the urine is acid; it is practically carnivorous; once a vegetable diet is taken the urine becomes alkaline, and, it is probable, decreases in quantity.

The activity of certain glands, such as the thymus, becomes considerably reduced as the animal grows, until they disappear at the adult period.

One characteristic of the young animal is the necessity for sleep; it is probably during slumber that the tissues make the immense strides noticeable during the first few weeks of life.

The period of dentition commences immediately at birth, if it has not already commenced *in utero;* the following table from Gamgee* shows the changes taking place in the teeth from birth to adult life:

KREUTZER'S TABLE OF DENTITION.

	Horse.		*Ruminants.*	
	Eruption.	*Change.*	*Eruption.*	*Change.*
Incisors:				
Central	Before or a few days after birth	2½ years	Before or a few days after birth	1½ years
Lateral	4 to 6 weeks	3½ years		2½ years
Outer lateral	—	—	14 days	3½ years
Corner	6 to 9 months	4½ years	2 to 3 weeks	4½ years
Tushes	4 to 5 years			
Molars:				
First	Before or a few days after birth	2½ years	Before or a few days after birth	1½ years
Second				2½ years
Third		3½ years		3½ years
Fourth	10 to 12 months	—	6 to 9 months	
Fifth	1½ to 2 years	—	2½ years	
Sixth	4 to 5 years	—	4 to 5 years	

* 'Our Domestic Animals.'

The influence of feeding on development is most remarkable: not only does the body increase in size and weight, but the animal presents the appearance of the adult, so that a thoroughbred at two years old is furnished and looks as old as an ordinary horse at four years old.

The completion of dentition marks the age of maturity; the uncastrated animal presents very distinctive features from the female, viz., greater bulk, a heavy crest and neck, and a harsher voice; the castrated horse more closely resembles the mare. No such difference as is observable in the human family exists between the male and female of the horse tribe: the mare arrives at maturity at the same time as the horse; and the castrated animal is not deficient in stamina, strength, or capacity for work; moreover, castration in the horse does not lead to a deposition of fat in the body.

Decay.—It is doubtful what age a horse would live to if not subjected to civilization; we may safely say that at seventeen years old the powers of life in the majority of animals are on the wane, though many at this period may be found in full possession of life and vigour; these are probably cases of the survival of the fittest, and cannot be taken as a general guide.

Doubtless the work performed by horses is the chief cause of their rapid decay; but apart from this, changes in their teeth, such as the wearing away of the molars, appear to preclude many of them from reaching a ripe old age, though instances are on record of horses attaining the age of thirty-five, forty-five, fifty, and one animal is known to have lived to sixty-two years of age.

Blaine* appears to have gone very carefully into the question of old age in equines, and he drew the following comparison:

'A parallel drawn between the ages of horses and of men will fully convince us of the error of fixing the decay of the horse at eight years from his birth. A very considerable attention to the subject, over a wide field of observation, has

* 'Encyclopædia of Rural Sports.'

impressed the writer with the propriety of drawing the following comparison between the ages of horses and men:

'The first five years of a horse may be considered as equivalent to the first twenty years of a man; or thus, a horse of five years may be *comparatively* considered as old as a man of twenty; a horse of ten years as a man of forty; a horse of fifteen as a man of fifty; a horse of twenty as a man of sixty; of twenty-five as a man of seventy; of thirty as a man of eighty; and of thirty-five as a man of ninety.

'So far from this comparison being too much in favour of the horse, we are disposed to think it too little so.

'Horses of thirty-five years of age are as common as men of ninety, provided it be taken into account there are at least fifty human subjects for every horse; and, unquestionably, a horse of forty-five is less rare than a man of a hundred and ten.'

Death.—Death from natural causes in the horse is a matter of rare occurrence; it is seldom that an animal is taken such care of that the tissues are worn out by age and decay, and the breath of life passes gradually from the body; by far the majority of horses meet either with a violent death or one the result of disease.

Natural death is described as commencing either at the heart, lungs, brain, or blood. Probably in the main most cases of natural death may be attributed to a failure of the heart's action; but from what we know of the physiology of the heart, respiration, and blood, it is very difficult to separate these in discussing the causes of natural death, knowing as we do how completely one is dependent on the other. The cessation of the heart's action may be looked upon as the termination of life.

We cannot enter upon the causes of death the result of disease, excepting to notice the interesting fact that no matter what the cause of death may be, horses seldom die quietly; by far the majority of them leave this world in powerful convulsions, fighting or struggling to the last, lying on their side, and galloping themselves to death. Rarely, indeed, does one witness a quiet death in horses,

and the subject presents a problem for the solution of the physiologist.

Shortly after death *rigor mortis* appears (see page 252), and within an hour or two tympany of the abdomen is apparent, reaching such a degree in a few hours, that post-mortem rupture of the diaphragm is exceedingly common. The explanation of this disturbance is the enormous amount of gas generated by vegetable food.

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